

# JOURNAL

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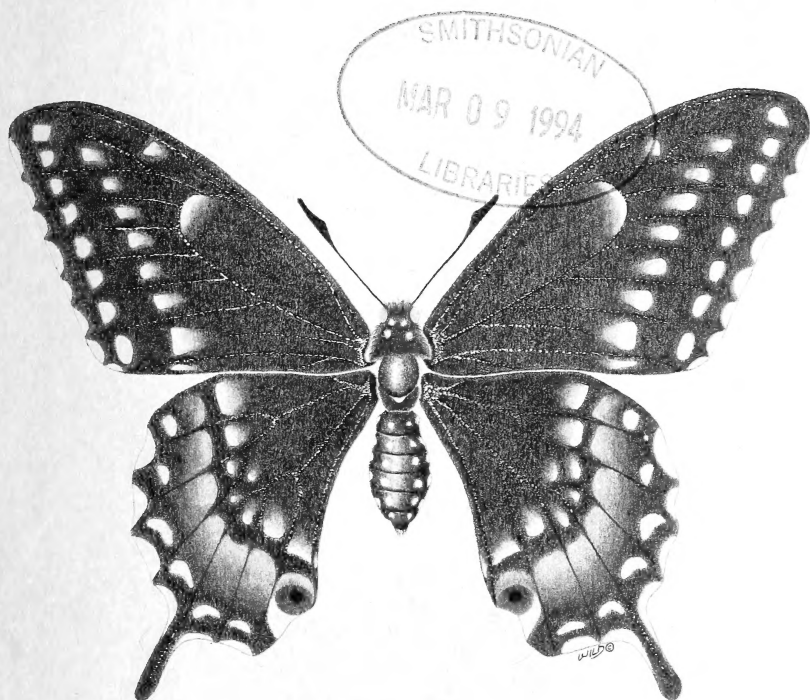
# LEPIDOPTERISTS' SOCIETY

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**Cover illustration:** The black swallowtail, *Papilio polyxenes asterius* (Stoll), is a widespread species of the eastern United States. The larvae feed on a variety of umbelliferous plants (Apiaceae). Original drawing by Erik Russell Wild, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045-2454.

# JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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## PRESIDENTIAL ADDRESS 1993: ON THE COMPARATIVE DISTRIBUTIONS OF LEPIDOPTERA AND LEPIDOPTERISTS

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Both Lepidoptera and lepidopterists, each part of a much larger group of similar organisms, represent but fleeting moments in time. But the Lepidoptera have flitted a great deal longer than we have as their students, by four orders of magnitude. I have been interested in the spatial and temporal distribution of butterflies for nearly 50 years, beginning in the neighborhood of my house and expanding incrementally to all of western North America (Stanford & Opler 1993), but began to notice a consistent artifact on the dot maps: butterflies are shown to be more common in cities, along paved roads, and in beautiful mountain meadows than in deserts, on farms, or in abandoned mine-fields. This presentation is an attempt to put these biases into perspective, based on several years' attempts by me and others to find out what species do occur (and even thrive) in the less-well-known habitats of our large region. Before summarizing my own research in this realm, it is necessary to give some historical perspective both on bugs and buggers.

Although some insect orders are known from fossils dating from early Cretaceous time, the first Lepidoptera appeared along with flowering plants about 120 million years before the present (mybp), and probably all families of Lepidoptera that exist today had differentiated by 66 mybp (Emmel et al. 1992). Most fossil butterflies date from the late Eocene to early Oligocene epochs, about 48-34 mybp, or later. Extensive movements of species occurred during and following the Pleistocene glaciations, as has been determined both from examination of fossils and study of today's distributions taking geologic evidence into consideration. Humans undertook equally extensive movements at the same time, extending into much of North and South America from

Eurasia perhaps as long ago as 35 thousand ybp. Lepidoptera appear in pictographs and caves dating from then, but it would be a stretch to refer to the artists as lepidopterists! The first drawings that are fairly easily determined to species are from Egyptian and Sumerian tombs from 5000 to 3000 ybp; *Danaus chrysippus* can be dated from drawings in Luxor created about 3500 ybp (Larsen 1990). The first surviving descriptions of Lepidoptera which may be considered scientific were by the Greek philosopher/scientist Aristotle, who lived and wrote in the 4th century BC. His accounts are sufficiently detailed that several species of butterflies and moths which still occur in his country could be considered described by him, but he failed to assign them Latin names or designate type localities! Common names (in Greek for *chrysippus*) are entirely appropriate for common species (Miller 1992), but are a conundrum for uncommon ones (Scott 1993) for which every author seems to make up a different common name. For example, what should be "Edwards' skipper"? He described 51 species of them (as presently classified) from the western United States alone. I shall not attempt to review the history of lepidopterists since the time of Linnaeus (1753), Cramer (1775), or Fabricius (1807), but the late F. Martin Brown wrote many historical papers in addition to his monumental series on the W. H. Edwards taxa. Brown influenced many of us over several decades, and I find it appropriate to dedicate my remarks here to his memory since he was long a guiding force behind my research.

Many factors influence the distribution of butterflies in space and time, including climate, host plants and other biological requirements, and the effects of human activity. In order for range maps to show the actual distribution of a species for any given interval of time, these factors and the potential biases and artifacts mentioned at the outset must be considered carefully. Also, the mapper must beware of introducing errors by the very process of making maps (Monmonier 1991), and the changes in a species' range over time require either several maps or different symbols denoting different time periods on a single map (e.g., Heath 1970). The British Atlas (Heath 1970) also shows different intensities of observation/collecting among the thousands of 10 km grid squares, so that the presence or absence of a species in a certain area may be evaluated in terms of observation density as well as other factors.

First off, I shall address the issue of errors which originate from the mapping process itself. All maps tell little white lies of necessity. Most of us grew up seeing Mercator-projection maps on classroom walls, where Greenland appears larger than the United States, and Antarctica is as long as the equator, but we learned quickly to adapt to these "lies." My well-worn Colorado highway map shows a prominent north-south



ribbon about 2 mm wide running from Cheyenne, Wyoming, to Raton, New Mexico, Interstate Highway 25. If that width were to scale, a DC-10 could easily land crosswise and never see or hit an automobile! Similar types of misinterpretation are possible on dot maps of small scale, where only a single dot in the center of each county (or other unit) will fit. For example, a common species such as *Vanessa cardui*, known from all counties of both Kansas and Nevada, appears to be very much more common in Kansas (105 tiny counties) than in Nevada (13 gigantic ones and 4 tiny ones) simply because the dots are nearly confluent in Kansas. Also, *Boloria acrocneuma* shows in 4 large Colorado counties, with a total area of thousands of square miles, but the insect actually occurs in only a few several-acre colonies above treeline on the San Juan massif. Of course, in a scientific paper addressing either of these issues, the maps would be prepared in different formats, with equal size grid squares for the painted lady in Kansas and Nevada, and a large scale map to show the specific localities for the Uncompahgre fritillary in Colorado. In a work with over 1000 identical-format maps, these matters must be summarized by a simple caveat in the introduction: Beware of [implied] lies! Most range maps, whether showing discrete dots or shading, are based on county records in the United States because the county of the locality on the specimen label is usually easy to determine given the other label data and ready access to historical maps; also there is no standard grid system used among disciplines, although longitude/latitude could be used. However, using counties as the basis requires considerable care to avoid plotting errors. Counties sometimes come or go, or change boundaries, or even names, and the names of towns correlate poorly with county names. Here are some examples. Before Colorado became a State in 1876, Denver was in Montana! That is, Montana Co., Kansas Territory. Several butterfly species were described from "Denver" which do not occur anywhere near the city and certainly didn't then either, so a dot must not be placed there without better information. Grand Co., Utah Territory, included what are now Grand Co., Colorado, Grand Co., Utah, and nearly everything in between. In more recent years, Washabaugh Co., South Dakota, vanished into Jackson Co., South Dakota (combining the map dots was quite easily accomplished), while Yuma Co., Arizona, and Valencia Co., New Mexico split into 2 counties each (we had to go back to ground zero for many records), and Denver Co., Colorado gobbled up a lot of real estate in Adams Co. (requiring transfer of a few county dots). Bullfrog Co., Nevada, was created and then abolished so quickly that no action was necessary on our part. Several of the Sierra foothill counties in California changed their boundaries almost weekly in the days of the Gold Rush and afterward, but have fortunately been stable during most of col-

A

CABBAGE WHITE (P. RAPAE), 1800LEPIDOPTERISTS, 1800

B

CABBAGE WHITE (P. RAPAE), 1956  
(Published records)LEPIDOPTERISTS, 1956  
(Lepidopterists' Society membership list)

C

CABBAGE WHITE (P. RAPAE), 1993LEPIDOPTERISTS, 1993 (Season Summaries 1983-1993)

lecting efforts there since the time of Lorquin. The Sonora blue, described from "Sonora," was from near the California gold camps, not Mexico! Then, beware of ambiguous and misleading names: Bent, Colorado, is in Las Animas Co., while Las Animas is the seat of Bent Co.; also Cheyenne Co. is in Nebraska, while Cheyenne, Wyoming is in Laramie Co., and Laramie, Wyoming is in Albany Co. (NOT New York)!

Secondly, maps reflect the habitats of lepidopterists at least as much as those of the Lepidoptera they study, and also the goals and biases of the students. I mentioned earlier that populated, easy-access, and beautiful places tend to be better known than unpopulated, remote, and barren ones, but another principle has been called Powell's Law for its perpetrator J. A. Powell: distant places are more thoroughly studied than close ones, or "No field biologist does any significant work closer than 1000 miles from his home!" A case in point could be the Chiricahua Mtns of Arizona, or the Galapagos Islands, but if one looks at the evolving knowledge of common species' distributions, the exact opposite seems to be true. I have chosen the cabbage white, *Pieris rapae*, to illustrate this point. Panel A of Fig. 1 shows the range of this introduced Eurasian species in 1800, several years before it first appeared on our continent, side-by-side with the range of serious lepidopterists in the same year in the western United States: both zero! Panel B shows the known locations for each group in 1956, again nearly the same, in cities and towns only. Panel C shows where they are documented to exist in 1993—again identical, but this time nearly everywhere. So my corollary to Powell's Law is the converse: "No one notices cabbage whites except in his/her own back yard!" Except that a certain map-dotter finally picked one up on the west side of Loveland Pass, Colorado, 12,000' above sea level, to complete the dots for all 63 counties and prove Powell correct after all. The distribution of lepidopterists also is shown by the fact that 110 butterfly species are known from Scott Co., Kansas, compared with 30 to 45 in surrounding and equally depauperate counties, because Virgil Calkins lived and recorded species in his back yard in Scott City for several decades this century. In his honor I have therefore formulated Calkins' Law: If one studies a habitat for long enough, more than 100 butterfly species will be found there. Anywhere! Another artifact is caused by the interests of the observers. Swallowtails and fritillaries are much better known (but probably NOT more widespread) than skippers or noctuid moths, be-

←

FIG. 1. County records for the cabbage white (*Pieris rapae*) (left column) and the distribution of lepidopterists (right column). A) 1800; B) 1956; C) 1993.



cause they are more popular. Methods of observers affect the results also; like authors who accept literature records or sightings show more polka dots than those who accept only captures with voucher specimens and extremely detailed label data (frequently only their own). I am not faulting careful work, and am sometimes annoyed at papers that show everything from soup to nuts thereby conferring a measure of credibility on frank errors that should be expunged, but I support a middle ground. Maps that are revised frequently, or are on computer files, can be updated to show deletions and corrections as well as additions and format changes.

Finally, I pose a somewhat rhetorical question: When do range maps reach their maximal utility? An important point is reached when all common species are known from all or most grid squares or counties, because it can be inferred then that the ranges of rarer species are well-known also since most biologists are more interested in them, and that a scattergram stray species (such as *Eurema mexicana*) has not been encountered very frequently but can pop up nearly anywhere. We are nearing that inflection point for western butterflies now, and a map showing *E. mexicana* for all counties from Canada to Mexico in a few centuries would tell a different sort of lie, unless the relentless march of Eurasian weeds and fungi into the region—replacing most native plant species—should allow this particular species to flourish continent-wide. Will the range maps for cabbage whites in the year 2093 in western North America look very much like today's, with a few more squares filled in, or will they look like those in 1800? In either case, the comparative distributions of common Lepidoptera and common people will finally be identical, but where will the uncommon ones be? Hopefully the uncommon lepidopterists will still be pursuing the uncommon insects, as Rindge urged in his 1965 presidential address, which I had the privilege to hear in person. Collect NOW, he urged, because it soon would be too late. His message is still true, and even more urgent than nearly 30 years ago. Much collecting is possible with a good telephoto camera, but museums and universities still need material, especially of yet unknown or poorly known species, so the process of obtaining permits to collect specimens is well worth the effort. When all that is left is cabbage whites, a permit will probably not be required. If so, the butterflies may have to issue it.

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## A NEW GENUS OF WINTER MOTHS (GEOMETRIDAE) FROM EASTERN CALIFORNIA AND WESTERN NEVADA

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**ABSTRACT.** *Tescalsia*, a new genus of Geometridae, is described and assigned to the subfamily Larentiinae. It is represented by two new species: *Tescalsia giulianiata* Ferguson, known from 3 localities in and adjacent to the Owens Valley, Inyo Co., California, and *T. minata* Ferguson, from Mineral Co., Nevada. The female of *T. giulianiata* has linear, straplike forewings, vestigial hindwings, and long, slender legs that enable agile climbing in shrubs; the female of *T. minata* is unknown. Both sexes lack the proboscis and tympana. Adults of *T. giulianiata* are active at sundown and nocturnally in November and December, despite near freezing temperatures.

**Additional key words:** brachypterous, flightless, Larentiinae, tympana.

In 1976 Mr. Derham Giuliani, a keen naturalist of Big Pine, California, brought a brachypterous moth to Berkeley that he had collected in Deep Spring Valley, east of Big Pine, in early December 1973. So bizarre was the specimen, with peculiarly bristled, straplike forewings and vestigial hindwings and mouthparts, that Powell could not identify it to family. The taxonomic placement remained a mystery after Ferguson and other lepidopterists at the National Museum of Natural History (NMNH) examined the specimen in 1977.

Two additional females were taken in pitfall traps at Deep Spring Valley in December 1978, one of which laid eggs that produced first instar geometrid larvae. After additional visits by Giuliani, Powell, and others during November and December 1978-82, we had assembled 9 winged males and 8 females, a sufficient sample to provide convincing circumstantial evidence for the association of the sexes. The males indicate that the mystery moth is an undescribed species best assigned to the Larentiinae (Geometridae).

Later, males of a congeneric species, from Mina, Mineral Co., Nevada, that had been collected in 1914, were discovered by Ferguson in unidentified material at the NMNH. Although descriptions of the new genus and species were written several years ago, we delayed publication, anticipating that the larva and host plant might be discovered; but that hope has not been realized. Hence, we present the descriptions, and characterize the egg, together with observations on the habitats and adult behavior.



## MATERIALS AND METHODS

**Trapping method.** The first female was observed on the sand, and a few males were netted near sundown; but most of the series was taken in pitfall traps. This technique is widely used for sampling ground-dwelling insects in various habitats and is particularly effective for nocturnal insects such as many beetles. Cups may be deployed empty, baited with truly disgusting materials, or partially filled with anti-freeze (ethylene glycol), which allows long-term sampling. If deployed empty, traps need to be checked frequently because many predators, spiders, scorpions, carabid beetles etc., are trapped.

We used 9 oz. squat plastic tumblers (7 cm deep and 9 cm diameter at the rim); they are inexpensive and nest in compact packages for transport. We deployed them in transect lines of 50–100, about 2 m apart, usually situated at the bases of shrubs. We trapped with empty cups during single nights (when two of three females were killed by a predaceous mite and spider) or with anti-freeze over a several day period. Specimens taken from the latter were washed in water, then transferred to alcohol, and later dried for pinning. Understandably, lepidopterists rarely are familiar with the method, but it is an effective one for brachypterous forms. Winged males are also sometimes trapped, and most of our male *Tescalsia* were collected this way. The holotype was taken in early morning in an empty trap about 50 m from the nearest trapped female.

## SYSTEMATICS

*Tescalsia* Ferguson, new genus

**Type species:** *Tescalsia giulianiata* Ferguson, new species.

**Diagnosis.** Characterized by the following combination of unusual characters: 1) in male, veins Sc and Rs fused for half length of hindwing, forking just before end of the very long cell, and beyond that point Rs and M<sub>1</sub> stalked together for  $\frac{1}{4}$  or  $\frac{1}{8}$  of distance from end of cell to outer margin; 2) female with greatly reduced forewing, linear and straplike, with numerous setae longer than width of wing along entire length of both fore and hind margins; 3) female with hindwing present only as a vestige concealed beneath base of forewing; 4) tympanic cavities in base of abdomen, characteristic of nearly all Geometridae, missing in both sexes; 5) proboscis missing in both sexes, as is true of some other winter moths.

**Description.** MALE: Length of forewing: 12.0–17.5 mm. Head: Antenna bipectinate, extremely delicate, with slender shaft and long, widely spaced, setose branches and large scape 3–4 times thickness of shaft;

shaft scaled dorsally. Labial palpus short, hardly extending beyond front. Eye not very large, its vertical length almost equal to width of front at narrowest point, but strongly protuberant in the type-species, less so in the other. Ocellus absent. Front protuberant, rounded. Chaetosema normal, moderately to well developed, the two chaetosemata not extended transversely to meet behind head as in many Larentiinae. Tongue absent. Vestiture untufted. Legs slender, normal except that foretibia is extremely reduced and bears a large, conspicuous, double claw (Fig. 9), and foretarsus much more elongated than mid- or hind-tarsus; hindtibia with one or two pairs of spurs.

Fore- and hindwing somewhat elongated, produced especially toward apex; tornus of both wings rounded; forewing length/width ratio about 2.4/1.0, narrower than the 2.0/1.0 ratio of *Operophtera* (length = base to apex; width = length of line through anal angle meeting costa at 90°); wing pattern mostly diffuse and indistinct, variable between and within species; hindwing maculation differing from that of forewing in its reduced pattern consisting of discal spot only or discal spot and diffuse postmedial band only; fringes of both wings unusually long; wings covered with wide, tulip-shaped to almost round scales, dentate with 3–5 short points distally or simple. Venation as described and figured (Fig. 8); Sc of forewing free from radials; discal cells long, that of forewing more than half and of hindwing about half length of wing, closed off almost straight transversely at ends; forewing with two large accessory cells; hindwing with discal cell unusually wide because of long fusion of Sc and Rs, with  $M_2$  a fully developed, tubular vein, and with 1st A a well-developed fold, 2nd A a well-developed vein, and 3rd A entirely lost. Frenulum well developed and very long.

Male genitalia (Figs. 10, 11). Valva and uncus simple; uncus appearing to be fused to tegumen, forming a solid unit; gnathos absent; transtilla distinct, forming slender, complete bridge; manica spinulate, heavily so in one species, flanked by pair of knoblike, setose processes, the derivation of which is unclear; each knoblike process with delicate, sclerotized connections both to juxta and base of costa of valva; juxta appearing to have a large, pointed, conical or thornlike medial process adjoining its posterior margin, seemingly apposed to end of aedeagus, and derivation of this structure also unclear. Vesica with clumps of small cornuti.

FEMALE (Fig. 14, type species only): Head: Antenna simple, slender, sparsely setose, with scape much smaller than that of male. Labial palpus small, not exceeding front. Eye nearly as large as that of male. Ocellus absent. Tongue absent. Front, chaetosema, and legs similar to those of male. Brachypterous; forewing 6–7 mm long,  $\frac{1}{2}$  to  $\frac{2}{3}$  length of body, narrow, straplike, tapering to a pointed end, roughly clothed

with scales narrower than those of male and with both margins fringed with long, straight, bristlelike setae slightly longer than width of wing; hindwing present as small vestige beneath base of forewing and bearing long setae distally. Venation (Fig. 12) very reduced but bearing three longitudinal elements that are probably the stems of Sc, R, and Cu.

Female genitalia (Fig. 13). Simple and without very significant features except an extremely long ostial cavity, with a pair of lateral sclerotized supports at base or in what may be a funnel-like posterior section of the ductus bursae, that on right side the larger; corpus bursae ovoid, membranous, delicate, without signum; ductus seminalis arising from bursa near ductus bursae. Sclerotized parts darkly pigmented.

**Distribution.** Known only from arid habitats of eastern California, and western Nevada.

**Early stages.** Eggs and first instar larvae were obtained, but larvae would not feed. Food plant unknown. Young larva typically geometroid, with no indication of a third pair of prolegs such as might indicate a relationship to the *Alsophila* group.

**Remarks.** Sattler (1991) has reviewed wing reduction in Lepidoptera and analyzed implications of flightlessness. Examples of brachyptery in female winter moths in the Northern Hemisphere are known in several families; they are particularly numerous in Geometridae (e.g., *Alsophila*, Oenochrominae; *Phigalia*, Ennominae; and *Operophtera*, Larentiinae). The taxonomic relationships of *Tescalsia* proved difficult to determine and are still not clear. A combination of such features as the double accessory cell, free subcosta, extremely long fusion of Sc + Rs in the hindwing, and condition of the anal veins, points to a probable connection with the Larentiinae. Because of the elongate discal cells, loss of the proboscis, and reduced tympanic cavities, the possibility of relationship to the *Alsophila* group (currently in the Oenochrominae but probably misplaced) was also considered. All species of *Alsophila*, as well as the similar *Phthorarcha primigera* Staudinger (Central Asia) and *Inurois tenuis* Butler (Japan), were examined. These agree with one another in venation, especially with respect to the anal veins of the hindwing consisting of a weak 1st anal fold and well-developed 2nd and 3rd anals. *Tescalsia* clearly differs in having a strong 1st anal fold, well-developed 2nd anal, but no 3rd anal. This would seem to relate *Tescalsia* to the Larentiinae, in which the Hydrimenini and Operophterini have anal veins of this type. Surprisingly, *Phthorarcha* has wide, rounded wing scales almost exactly like those of *Tescalsia*, although other members of the *Alsophila* group and Larentiinae examined do not.

The venation agrees best with that of the Larentiinae, although it is of an exaggerated type with two large accessory cells, elongated discal

cells, and elongated fusion of Sc and Rs in the hindwing, and the almost straight, transverse closure of the ends of the cells is unusual. The genitalia, both male and female, seem closer to those of *Operophtera* than anything else, the male genitalia are quite like those of *Operophtera* in general form, in the shape of the valvae, and in the apparent homology of all components of the anellus. In female *Operophtera*, the beginnings of the same kind of large ostial cavity and short, sclerotized ductus bursae are apparent, and the simple, membranous corpus bursae, lacking a signum, agrees exactly. *Operophtera* has fairly well-developed tympanic cavities in the base of the abdomen, but their loss, together with the loss of the tongue, extremely wide pectinate male antennae, and curiously specialized female wings are adaptations to an extreme habitat. The large foretibial claw appears here and there in many groups of geometrids and noctuids, especially of desert habitats, and it has no important systematic significance. A palearctic geometrid that occurs in winter in Turkmenia and Kazakhstan, *Cheimoptera pennigera* Danil. (Danilevskiy 1969) shows many of the same features, including the foretibial claw and loss of the tympanic cavities, although it is unrelated to *Tescalsia* and believed to belong to the Ennominae. *Tescalsia* should, for the present, be assigned to the tribe Operophterini of the Larentiinae, although there are notable differences. For example, other species of Operophterini possess a reduced proboscis, large chaetosemata that meet in the middle in some instances, coarsely ciliate rather than bipectinate antennae in the male, lack the foretibial claw, and have either one accessory cell in the forewing (*Operophtera*), or two (*Epirrita*) as in *Tescalsia*.

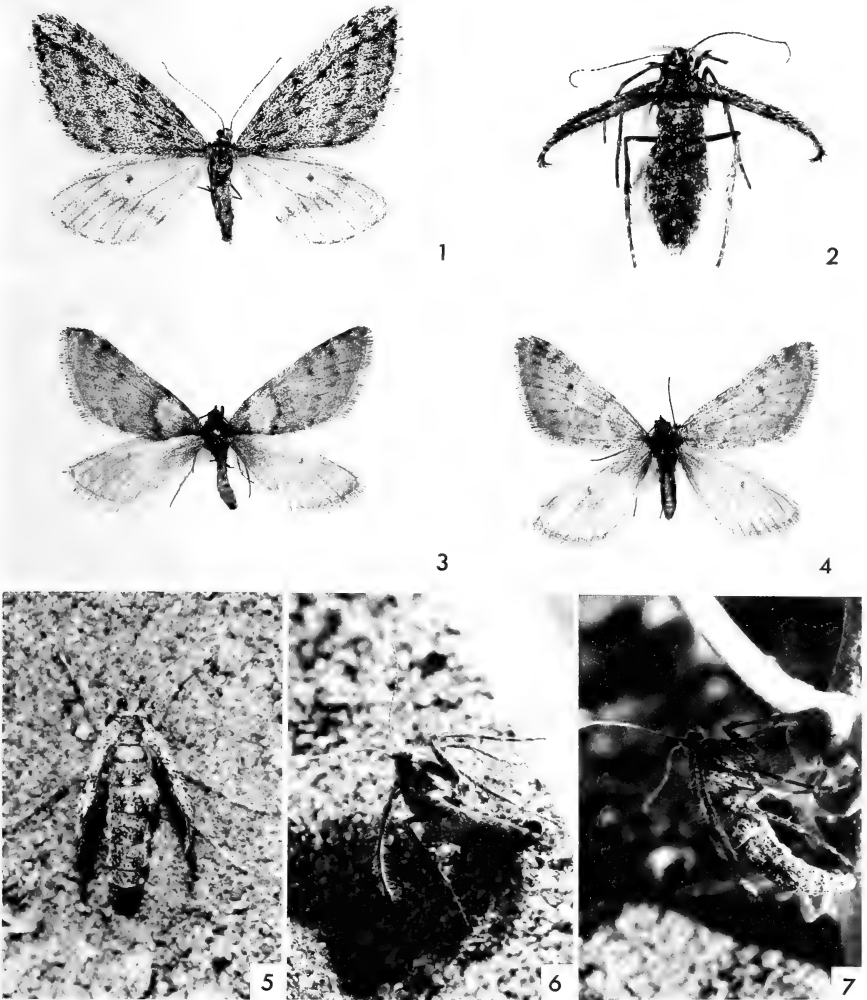
The superficially similar, gray, long-winged *Chesiadodes morosata* Hulst (Ennominae) flies in the same area near Lone Pine, Inyo County, California, in December, and also has a foretibial claw, although of different shape. It differs in having a proboscis. The two are not closely related, and the female of *Chesiadodes* has fully developed wings.

***Tescalsia giulianiata* Ferguson, new species**

(Figs. 1, 2, 5-9, 11-14)

**Diagnosis.** Males large, forewing length 16.0-17.5 mm; wings gray with blackish markings; hindtibia with two pairs of spurs. Female as described for genus and illustrated.

**Description.** MALE: Head: labial palpus small, not surpassing front; eye of about same dimensions as that of *T. minata* but more protuberant, its form exceeding that of half a sphere; front bulging, roundly convex, with large, broad, gray-brown or whitish scales, tending to be oriented toward middle of front; eye rimmed anteriorly and ventrally with



FIGS. 1-7. 1, *Tescalsia giulianiata* Ferguson, holotype male. 2, *T. giulianiata*, paratype female (same data as holotype). 3, *T. minata* Ferguson, holotype male; 4, *T. minata*, paratype male. 5-7, *T. giulianiata*, female (Deep Spring Valley, CA, XII-15-78): 5, perched on sand; 6, in repose balanced on wingtips; 7, climbing on *Chenopodium* branch.

contrastingly pale border of radiating whitish scales. Thorax beneath without long, hairlike scales; legs similar to those of *T. minata* except that femora lack long, hairlike scales, and hindtibia has two pairs of spurs. Wings whitish, dusted with blackish scales and thus appearing gray, although forewing sometimes so heavily suffused that markings are obscured; forewing normally with diffuse, slightly dentate or sinuous

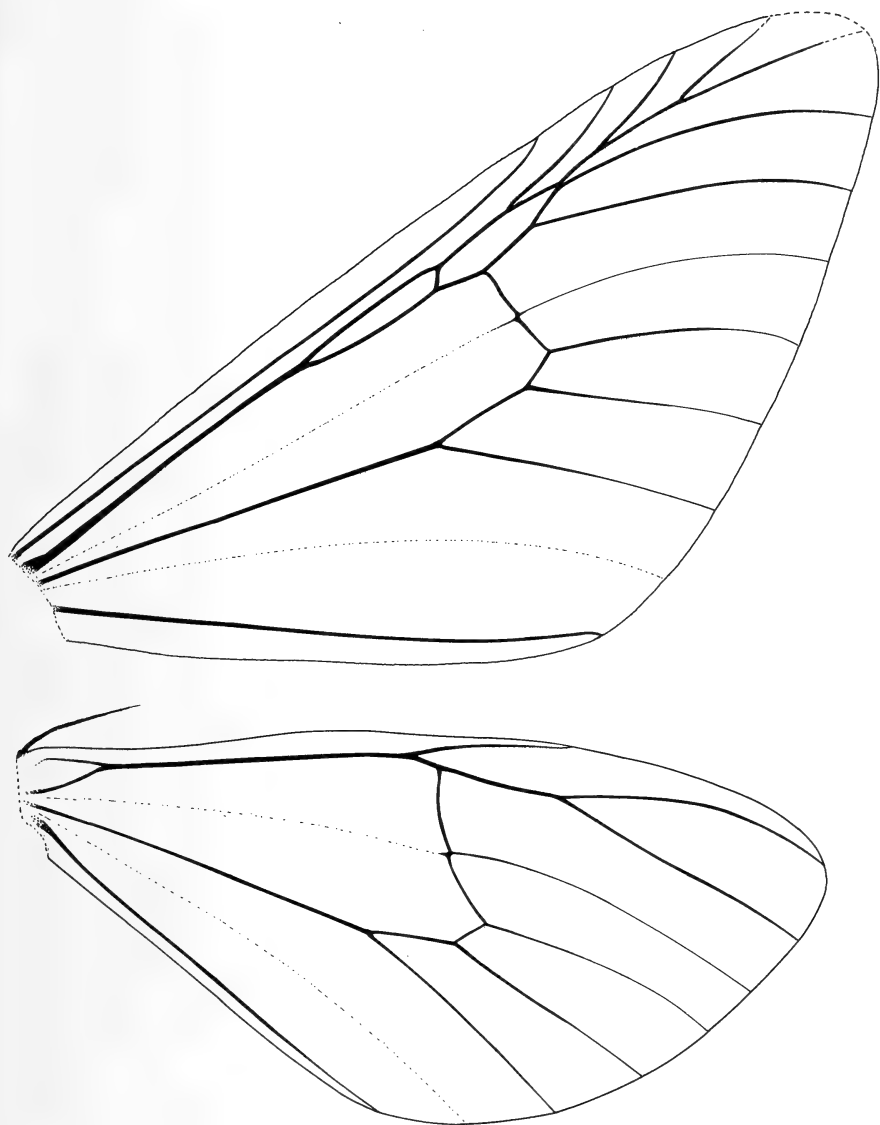


dark antemedial and postmedial bands, the former slightly convex and subparallel to postmedial, which is nearly parallel to outer margin; subterminal shade, if present, indistinct, similarly parallel to outer margin; some veins, especially in medial area, faintly outlined with dark scales; black discal spot present; fringe white, checkered with dark brown and preceded by weak terminal line of diffuse dark spots. Hindwing paler gray, almost unmarked except for small discal spot and diffuse but complete transverse band crossing just beyond middle of wing; fringe whitish, unmarked, preceded by faint, broken terminal line in some specimens. Underside with fore- and hindwing nearly alike, light gray with discal spots, diffuse postmedial bands, and variable, black, interrupted, terminal lines. Length of forewing: holotype, 17.0 mm; other ♂, 16.0–17.5 mm. Genitalia (Fig. 11), differing from those of *T. minata* mainly in their wider, blunt or obtusely pointed medial juxtal process, less heavily spined manica, and smaller, paired, setose processes attached to bases of costal sclerite. Eighth sternite rectangular, not triangular, and eighth tergum without a posterior border of persistent scales.

**FEMALE:** As described for genus. Antenna simple, covered with whitish scales. Hindtibia with two pairs of spurs. Body gray, variably dusted with black scales; in paler specimens a pair of dark subdorsal spots toward posterior margins of abdominal segments 2–5. Legs gray brown with each tarsal segment pale-tipped. Forewing with light and dark scales almost evenly mixed and no other markings. Length of forewing: 5–6 mm. Genitalia (Fig. 13) as illustrated and described for genus.

**Types.** Holotype male and allotype female: CALIFORNIA, Inyo Co., Alabama Hills, 4 miles [5 airline km] southwest of Lone Pine, 4550' [1390 m elev.], 6/7-XII-1982, in pitfall traps (J. De Benedictis & J. Powell); deposited in Essig Museum of Entomology, U. California, Berkeley. Paratypes (15), all Inyo Co., CA: 4 ♂, 3 ♀, same data as holotype, 7/11-XII-1982 (D. Giuliani, De Benedictis, Powell); 1 ♂, Alabama Hills, N. fork Lubkin Cr., 4 mi. S, 1 mi. W of Lone Pine, 4300', 11-XII-1982 (Giuliani); 1 ♀, Deep Spring Valley, 8-XII-1973, sand dunes (Giuliani); 2 ♀, same locality, 15/16-XII-1978, pitfall traps (Powell); 1 ♂, same locality, 17-XI-1980, flying at sundown (Giuliani); 2 ♂, same data, 17-XI-1982; 1 ♀, Owens Lake, mid XI to mid XII-1978, ethylene glycol pit trap, *Atriplex-Franseria* assoc. (Giuliani, F. Andrews, D. Hardy); paratypes deposited in California Dept. Food & Agric., Sacramento, Essig Museum, and U.S. National Museum of Natural History, Washington, D.C.

**Habitats.** *Tescalsia giulianiata* is known from three sites in the Owens Valley region, California, which are similar in general aspects of veg-



8

FIG. 8. *Tescalsia giulianiata* Ferguson, male, wing venation.

etation architecture, with a low scrub of scattered shrubs interspersed with open patches of sand, yet they differ in dominant plant species.

1) Deep Spring Valley is a closed basin at 1500–1600 m elevation, situated southeast of the White Mountains and surrounded by arid

mountain ridges. To the west the valley is separated from the Owens Valley by Westgard Pass (2225 m) and to the east from the valleys of Nevada by Gilbert Summit (1950 m). From the highway along the north edge of the valley, the terrain slopes southward towards Deep Spring Lake, which is dry except following winter storms. Fine aeolian sand from the dry lakebed has been deposited to form low ridges and dunes that are stabilized by low scrub dominated by *Atriplex confertifolia* (Chenopodiaceae), *Thamnosma montana* (Rutaceae) and scattered patches of *Chrysothamnus nauseosus* (Asteraceae). Female moths were taken from open sand and in pitfall traps placed at the base of *Atriplex* and *Thamnosma*, about 1 km north of the lakebed.

The valley is about 300 m above the floor of Owens Valley, and it evidently acts as a basin for cold air drainage, with snow patches persisting much longer than at comparable elevations on the hills around Owens Valley. During our December visits, daytime temperatures of 10–13°C fell rapidly, to 4.5–5.0°C towards sundown and 1.6–4.5° by dusk.

2) The Alabama Hills are remnants of an ancient uplift that has eroded to low hills of decomposed granitic, alluvial sand subtending weathered, granite outcrops. The collecting site is situated at 1390 m elevation about 5 airline km southwest of Lone Pine, off Indian Springs Road. This area is characterized by gently sloping expanses of coarse, granitic sand stabilized by a low scrub consisting mainly of *Tetradymia glabrata* (Asteraceae), a low spiny *Atriplex*, and scattered *Chrysothamnus nauseosus*. Most of the type series was taken at this site, December 7/11, 1982, in pitfall traps deployed December 6. Although the locality is only about 100 m lower than Deep Spring Valley, it is a much warmer habitat during winter.

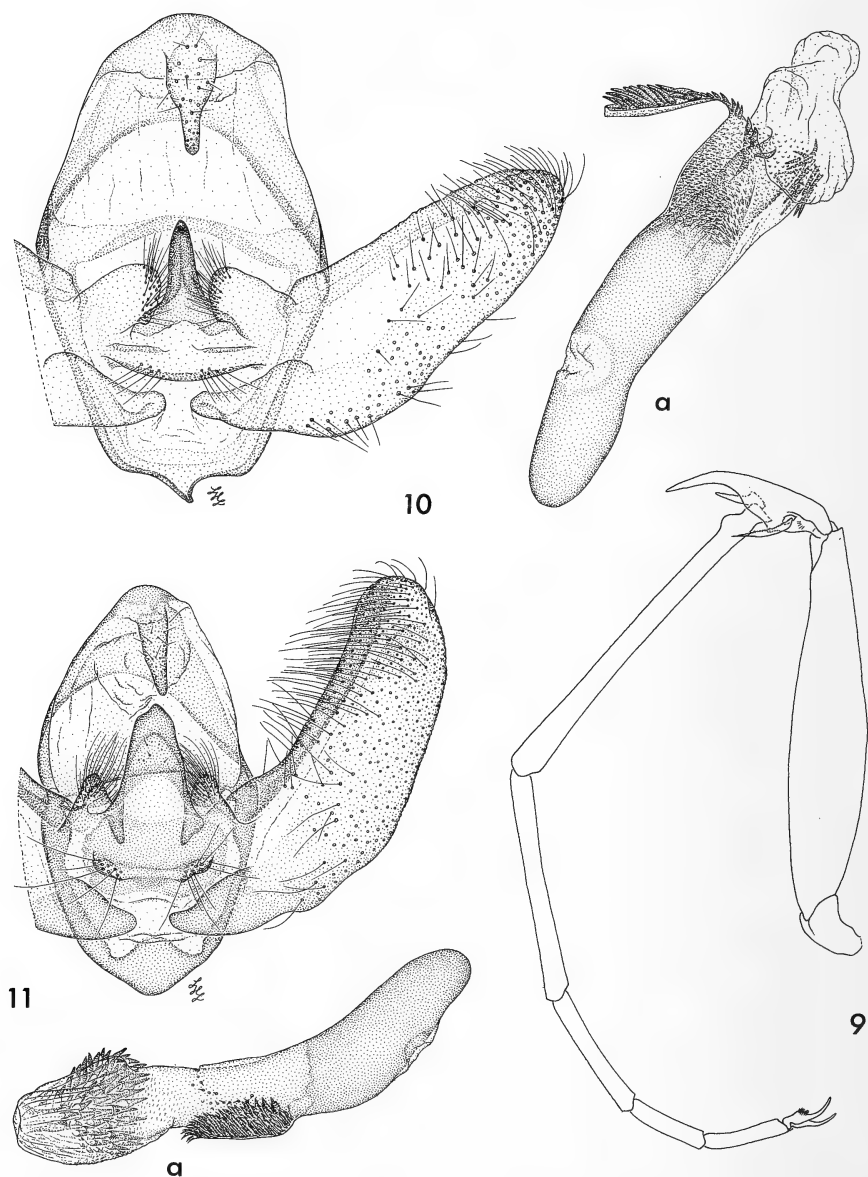
3) The former Owens Lake was drained by the Los Angeles water district, beginning in the 1920's, and has long been a dry lakebed. Aeolian sand is deposited in low ridges along its east margin. One female of *T. giulianata* was taken here in a pitfall trap. Giuliani and F. G. Andrews had monitored the area by pitfall trapping, with 12 traps in each of 7 vegetation types for one year. The site that yielded the *Tescalsia* is about 3 km northwest of Keeler (1100 m). The traps were set east of a few low sandhills at the margin of the lakebed, in a low area that acts as a catch basin for the sparse rainfall runoff. It is characterized by shadscale scrub, alkaline tolerant species of Chenopodiaceae, including *Atriplex hymenelytra*, the spiny *Atriplex* of the Alabama Hills, *Allenrolfia occidentalis*, and *Sarcobatus vermiculatus*, as well as *Tetradymia glabrata*. Thus the dominant vegetation is more similar to the Alabama Hills site than to Deep Spring Valley. We did not deploy additional pitfall traps at this locality after, 1978.

**Diel rhythm.** Temperatures in December in the Owens Valley area typically drop to 2–10°C below freezing at night but rise well above freezing during the day, often to 10–15°C. Nonetheless, our observations suggest that *Tescalsia giulianiata* is not diurnal and begins activity near sundown. Its period of activity may vary daily with a low temperature threshold and may exclude some evenings. Males were observed flying only twice, by Giuliani on November 17, 1980 and Nov. 17, 1982, near sundown. One female was found on open sand in late afternoon, and one was trapped in a pitfall between 1530–1615 PST (ca. 8–10°C; sunset at 1610), and another between 1630 and 1030 PST the following day, in temperatures below 5°C. Other individuals were trapped during longer intervals, including one male and a female at the Alabama Hills between 1230 and 0930 the following day. Mating was not observed.

On each of the four dates in December, 1977–82, we made continuous observations for 2–8 h, on days when temperatures rose from 0.5–2.7°C at 0930–1030 PST to 15°C in mid afternoon, dropping to 4.5–5.0°C by sundown. No males were seen, and just one female was trapped during these intervals, which included extensive pitfall trapping, beating of shrubs, sifting and net brushing of the sand. *T. giulianiata* evidently is not adapted to diurnal flight when temperatures are highest. We ran a blacklight trap just once; the temperature was 4.5°C at dusk, and not one insect was trapped.

One captive female survived more than 4 days, with lab temperatures at 10–14°C at night to 21°C diurnally. Activity periods were sporadic, but in absence of disturbance, she seemed most active during evening, 1800–2100 h, moved only slowly when viewed by flashlight at 0500–0700, and rarely during morning hours.

During periods of activity, the female held the antennae and forewings at about a 45° angle to the plane of the body (Figs. 5–7). When quiescent, she positioned the antennae back along the body, and the wings were curled downward. On the sand surface, she seemed very awkward, scarcely able to ambulate forward or walk evenly. Walking on the sand, she dragged her abdomen, leaving linear tracks, but this did not seem to be a part of oviposition behavior. By contrast, when debris or the branchlet was encountered, she climbed quickly with agile movement from twig to twig and often hanging by one or two legs, reminiscent of a miniature orangutan. She frequently perched on the highest reach of the branchlet and moved quickly to maintain that position if the branch was moved. It seems that the species is adapted to life in shrubs rather than on the sand, which fails to explain why females were trapped in pitfalls but none could be beaten from shrubs. In fact, there may be strong selection against life on the sand at that time of year because predaceous mites and lycosid spiders appeared in



FIGS. 9-11. 9, *Tescalsia giulianiata* Ferguson, female, right prothoracic leg; small process arising near middle of double clawed tibia is a vestigial epiphysis. 10, *T. minata* Ferguson, male genitalia; a, aedeagus. 11, *T. giulianiata*, male genitalia; a, aedeagus.

33–50% of our pitfall traps. Two of the female *T. giulianiata* fell victim to these predators overnight, when we used dry cups.

Whether on sand or on twigs, the fore tarsi were extended, so that the tibial hooks were well back from the substrate; evidently they are not employed in adult locomotion. Upon disturbance, the female consistently feigned death, falling on her side with all legs retracted, and remained so for 10–20 seconds. Also, at times the female assumed a repose stance, balancing on her wingtips and curled abdomen, with the legs partially folded (Fig. 6). This may have been an abnormal behavior in confinement, but it was repeated several times for lengthy periods.

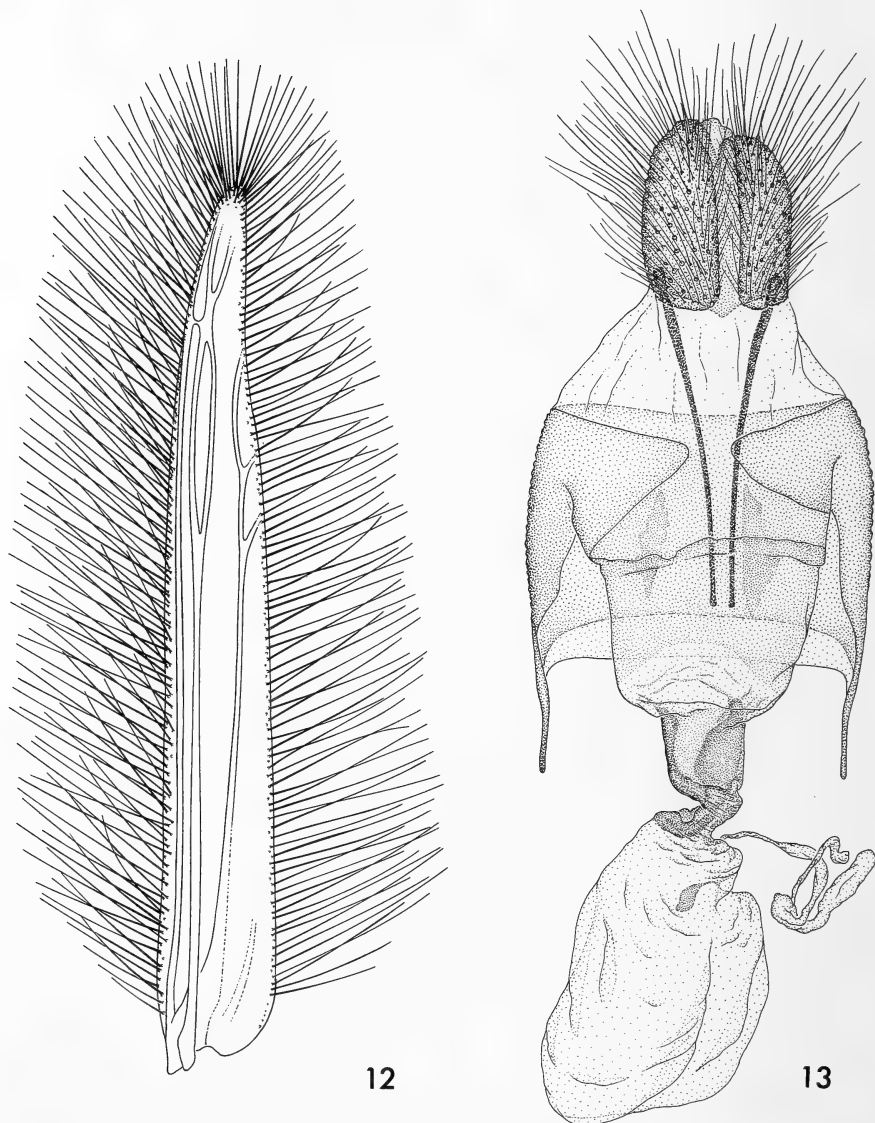
**Oviposition.** The single female retained alive was housed in a plastic box with sand and a dry branch of *Atriplex* (JAP 78M1). A cotton wick was provided, but there was no indication that the female ever imbibed moisture or touched the cotton with her vestigial mouthparts. She deposited 10 eggs in captivity, none during the first 48 h, 7 in the 3rd 24-h period, and 3 the following day. Eggs were deposited between 0940–1000 PST (1), 1055–1125 (1), 1400–1700 (6), and one later. Most were placed on loose sand, but the female was not observed to probe the sand with her abdomen. Two eggs were deposited on the damp cotton wick after the female had been coaxed onto it, and one egg was affixed to a dry *Atriplex* leaf.

Cuming (1961) reported the activity periods of the related larentine winter moth, *Operophtera brumata* (L.), to be nocturnal. Caged moths in outdoor conditions mated between 1730–2305 at temperatures of  $-0.8$  to  $+12.2^{\circ}\text{C}$ , and females oviposited between 1515–0020 at  $-1.6$  to  $+12.2^{\circ}\text{C}$ . *T. giulianiata* displays a comparable diel rhythm and temperature tolerance.

**Eggs.** The eggs ( $n = 10$ ), which were deposited singly, were oblong, slightly variable in shape, 0.80–0.90 mm long  $\times$  0.60 mm wide  $\times$  0.48 mm thick, somewhat flattened on the side away from the substrate. The chorion was opaque, white, very weakly rugose, appearing smooth under low magnification. When first deposited the eggs were pale greenish, similar in color and shape to new leaves of *Atriplex confertifolia*.

The eggs were confined in individual gelatin capsules; five were placed in a tightly covered plastic container in refrigeration each night (ca. 8:16 h,  $1.6^{\circ}$ :  $15$ – $20^{\circ}\text{C}$ ), while the remainder were retained at lab temperatures ( $10$ – $20^{\circ}\text{C}$ ), for 30 days. During development, eggs darkened and most showed a depressed area away from the micropylar end as though collapsing. Larvae began eclosing in the refrigerated subplot January 21, after 34 days; the others were refrigerated 8:16 h from day 36 to 46, and first instar larvae emerged February 2–4, after 46–48 days.





FIGS. 12-13. 12, *Tescalsia giulianiata* Ferguson, female, forewing showing setation of margins and rudimentary venation. 13, *T. giulianiata*, female genitalia.

**First instar larvae.** The eclosing larva ate a ragged, round hole at the micropylar end but did not continue to feed on the chorion. Each was placed in a small cup with synthetic diet (modified Shorey Diet used for *Choristoneura*) and a sprig of fresh *Atriplex* (but not *A. confertifolia*) from the U. C. Botanic Garden. None fed. After two days,

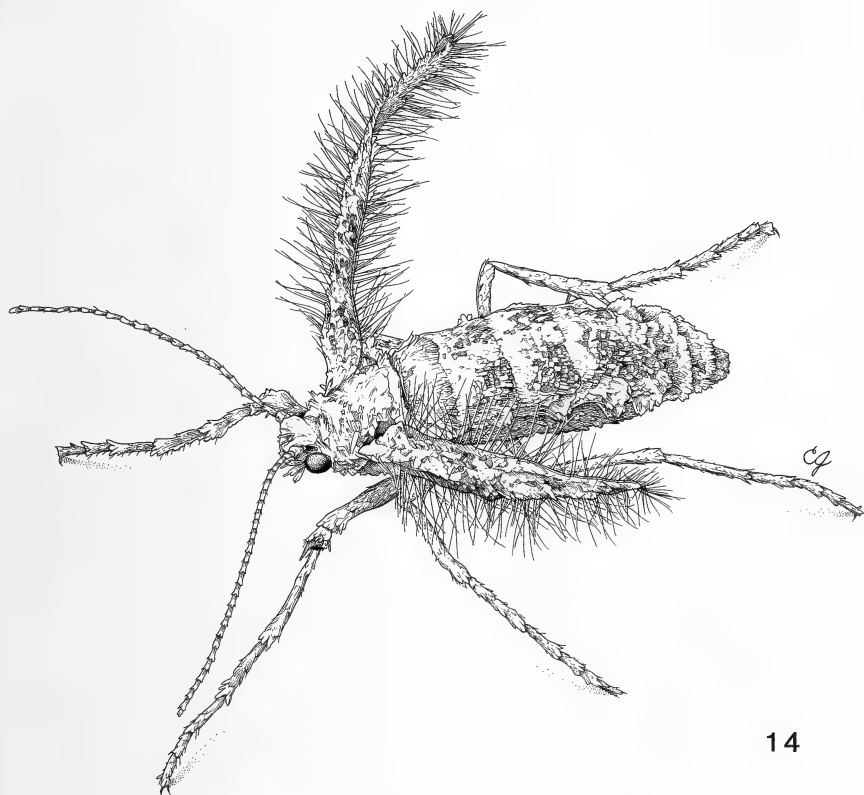


FIG. 14. Adult female of *Tescalsia giulianiata*.

some larvae also were offered a sprig of *Prunus* or *Salix*, but by that time they likely were too weak to feed. All died by the 3rd day after eclosion.

If failure to accept synthetic diet and the plants provided indicates a narrow host specificity, we cannot suggest a probably food plant. In retrospect, after observing the three habitats from which the flightless females were taken (just the one site was known at the time the eggs were obtained), *Atriplex* is the most plausible of the dominant, woody shrubs, with one or more species occurring in all three habitats. *Chrysothamnus*, which was present only in scattered patches, or some herbaceous perennial are possible alternative candidates.

***Tescalsia minata*, Ferguson, new species**

(Figs. 3, 4, 10)

**Diagnosis.** Males small, forewing length 12–15 mm; wings brown with mostly indistinct, darker brown markings; hindtibia with one pair of spurs. Female unknown.

**Description.** MALE: Head: labial palpus slender and delicate, but with its terminal scales clearly surpassing front; eye about as in the other species but much less protuberant, its shape distinctly less than that of half a sphere; front somewhat protuberant but flattened rather than roundly convex, with large, broad scales tending to be oriented toward middle of front; eye rimmed anteriorly and ventrally with brown scales concolorous with those of front, not contrasting. Thorax beneath and tegulae above sparsely clothed with long, brown, hairlike scales; legs similar in the two species except that femora of *T. minata* have long, hairlike scales, and the hindtibia only one pair of spurs. Wings gray brown with variable, darker brown markings; forewing with antemedial band often strongly convex and enclosing a paler area toward base; faint basal band also may be present; postmedial not always distinct but, if present, not parallel to outer margin, more curved, concave in posterior half of wing and convex in costal half; a vague, pale, subterminal band may be present; dark-brown discal spot present but weak; fringe brown, concolorous with wing, unmarked; terminal line wanting. Hindwing brown, hardly paler than forewing, unmarked except for weak discal spot; fringes concolorous. Underside much like upperside except that a faint, diffuse, convex, transverse band may cross just beyond discal spot, and veins on underside of hindwing may in part be faintly outlined with darker brown scales. Length of forewing: holotype, 13 mm; other ♂, 12–15 mm. Genitalia (Fig. 10), similar to those of *T. giulianata*; the most obvious difference is in the shape of the large medial process of juxta. In *T. minata* it has an abruptly acuminate, thornlike shape, with a sharp-pointed apex. Spines on manica more numerous and larger, and paired, setose processes flanking manica and adjoining base of costal sclerite of valva are larger. Eighth sternite small and triangular rather than quadrate, and eighth tergum with wide, dense tuft of short, persistent scales along its posterior margin, not easily removed in dissection.

FEMALE: Unknown.

**Types.** Holotype ♂, Mina [Mineral County], Nevada, November 17, 1914, A. Wetmore. Paratypes: 4 ♂, same data. Type series in collection of U.S. National Museum of Natural History, Washington, D.C.

#### ACKNOWLEDGMENTS

The discovery of this genus and subsequent important collections were made by Derham Giuliani, of Big Pine, California, who has contributed considerably to our knowledge of the insects of the interior deserts in California. F. G. Andrews, California State Department of Food & Agriculture, Sacramento, provided support for pitfall trap sampling by Giuliani. J. A. De Benedictis, now at University of California, Davis, J. T. Doyen, J. K. Liebherr, now at Cornell University, Ithaca, New York, endured winter field trips while at Berkeley. The genitalia and wing venation drawings were done by Linda H. Lawrence, Staff

Illustrator, Systematic Entomology Laboratory; the habitus drawing by Tina Jordan, U. California, Berkeley. The photographs of specimens were made by Ferguson and those of living moths by Powell.

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## SPLIT SKIPPERS: MEXICAN GENUS *POANOPSIS* GOES IN THE *ORIGENES* GROUP—AND *YVRETTA* FORMS THE *RHESUS* GROUP—OF *POLITES* (HESPERIIDAE)

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**ABSTRACT.** Genitalia show that the montane Mexican genus *Poanopsis* Godman fits snugly within the *origenes* group of *Polites* Scudder and that *Yvretta* Hemming constitutes a new species group of *Polites*. Relationships have been masked in part by evolutionary reduction and loss of various characters. The *origenes* group, with the northern superspecies *Polites mystic* (*P. mystic* (Edwards) + *P. sonora* (Scudder)), the intermediate linking species *P. origenes* (Fabricius), and the southern sister species *P. puxillius* (Mabille) **new combination** and *P. pupillus* (Plötz) **new combination**, extends from the width of southern Canada to southern Mexico. The *rhesus* group of *Polites*, with *P. rhesus* (Edwards) and the sister species *P. carus* (Edwards) and *P. subreticulata* (Plötz) (**new combinations**, all), extends from southern central Canada to Panama. Geographic distributions of species within these groups (and in the *themistocles* and *vibex* groups of *Polites*, as well) still strongly reflect allopatric speciation.

**Additional key words:** genitalia (male and female), variation, generic limits, character reduction and loss, speciation (allopatric).

In dealing with biodiversity, systematists divide and conquer. Formally described divisions assume a life of their own. The longer they live and the more we use them, the sounder they seem. Sometimes we get so accustomed to overly fine divisions that we cannot see the forest for the trees. The American genus *Polites* Scudder is one such forest, a good bit larger and denser than we thought.

Once upon a time, Godman (1900) created *Poanopsis* for a small, brown, high montane, Mexican skipper, *Pamphila puxillius* Mabille, which he made the type of his monotypic new genus. He observed that *puxillius*, with its short, broad wings, looks like *massasoit* Scudder, the type of the genus *Poanes* Scudder (hence the name *Poanopsis*), but differs conspicuously in having an oblique stigma on the forewing of the male from the origin of vein 3 to vein 1. Godman (1900:pl. 93, fig. 40—my Fig. 1) illustrated the male genitalia of *Poanopsis puxillius* without comment. In mid century, Evans (1955) added a similar Mexican skipper, *pupillus* Plötz (= *catahorma* Dyar), to *Poanopsis*, caricatured the male genitalia of both species, and set *Poanopsis* next to *Poanes*, eight genera removed from *Polites*. However, genitalia show that both species of *Poanopsis* belong in one of the species groups of *Polites*.

*Polites* is a familiar, widespread, New World genus, stretching from Canada to central Argentina, from Atlantic to Pacific coasts in both Americas, and through much of the West Indies. On the basis of genitalic



FIG. 1. Male genitalia of *Polites puxillus* (minus left valva) in left lateral view (ex Godman 1900:pl. 93, fig. 40). This figure presents the inner surface of the right valva whereas those that follow present the outer surface of the left valva. The specimen is "from the high tablelands of MEXICO."

and stigmal characters, MacNeill (1993) recognized four subdivisions: the *themistocles* group, the *origenes* group, the *vibex* group, and *Polites baracoa* (Lucas). He pointed out that, within groups (the *themistocles* group in particular), genitalia may be so conservative and so individually variable that differences between species blur but that, paradoxically, superficial color pattern will distinguish some of the genitalic look-alikes.

#### THE ORIGENES GROUP OF *POLITES*

The *origenes* group contains the eastern and central North American *Polites origenes* (Fabricius) plus the continent-spanning and largely allopatric sisters *P. mystic* (Edwards) and *P. sonora* (Scudder), all of which show some internal differentiation. From an evolutionary perspective, *P. mystic* and *P. sonora* can be considered a superspecies (see Stanford & Opler 1993:74, 75 for maps that more or less reflect the mutual geographic replacement of these two similar species, and see Burns 1964, 1983 for detailed analyses of superspecies in other American skippers). The *origenes* group ranges from Canada to the southern United States and, disjunctly, to higher elevations in the Sierra San Pedro Mártir of Baja California Norte, Mexico. Now, with *Polites puxillus* **new combination** and *Polites pupillus* **new combination**, it jumps from three to five obvious species and from the southern United States to southern mainland Mexico. Though these five species vary greatly in facies, they are genitally close, especially in males.

To be sure, male genitalia are grossly similar throughout the genus *Polites* (see figures in Scudder 1889, Skinner & Williams 1924 [or Lindsey et al. 1931], MacNeill 1993). Of all parts, the aedeagus is most generally useful in clustering species. Its accessories at once stamp the *origenes* group: the paired, toothed titillators are large, boldly dentate plates, something like semicircular saws (Figs. 1–5), extending downward from the lower part of the flared, distal end of the aedeagus (Figs. 1, 3, 5); and the lone cornutus is a rolled scroll bearing a crown of thorns (Figs. 2–5). In all other *Polites* the paired, toothed titillators assume

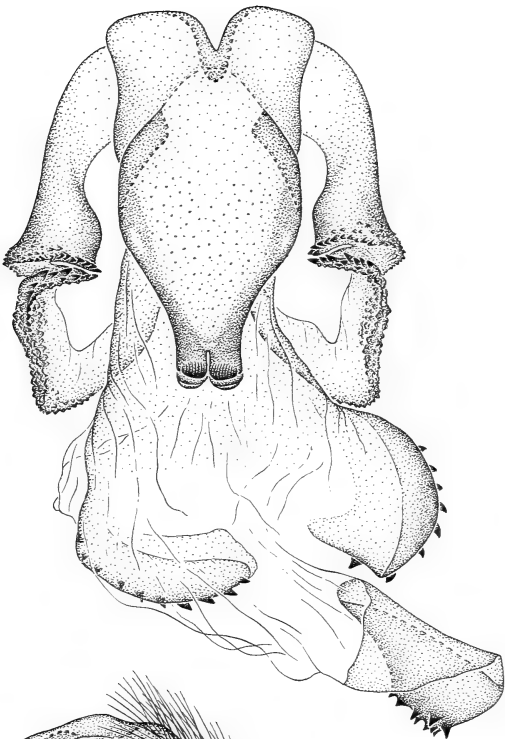




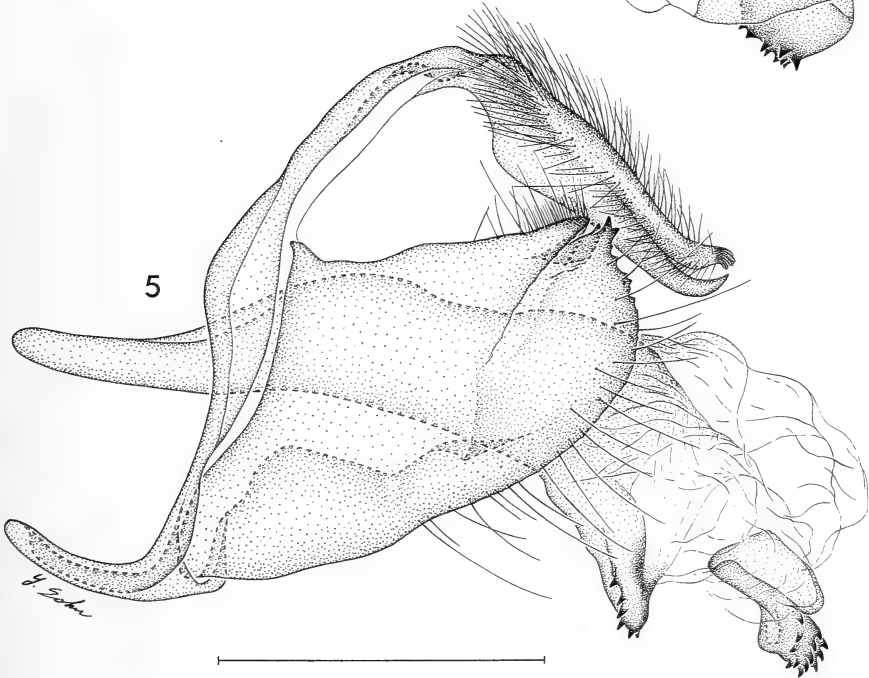
FIGS. 2, 3. Male genitalia of *Polites puxillus* from 28 mi (45 km) E El Salto, 8400 ft (2560 m), Durango, MEXICO, 6–7 August 1972, Viers & MacNeill [genitalia dissection number X-2652] (USNM). Scale = 1.0 mm. **2**, Tegumen, uncus, tip of gnathos, both valvae, both titillators (each with four teeth), and the single cornutus (like a rolled scroll bearing a crown of thorns)—all in posterior view; **3**, Complete genitalia (minus right valva, right titillator, and juxta) in left lateral view, with vesica everted.

FIGS. 4, 5. Male genitalia of *Polites pupillus* from Sierra de Guerrero, MEXICO, July 1913, R. Müller [X-2699] (USNM) (type of *Amblyscirtes catahorma* Dyar). Scale = 1.0 mm. **4**, Tegumen, uncus, tip of gnathos, both valvae, both titillators (left with 10 teeth, right with 8), and the single cornutus (like a rolled scroll bearing a crown of thorns)—all in posterior view; **5**, Complete genitalia (minus right valva, right titillator, and juxta) in left lateral view, with vesica everted.

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very different shapes, come from the upper (rather than lower) part of the distal end of the aedeagus, and, if they extend anywhere, extend backward (not downward); decorated cornuti number two or three (instead of one) and suggest thorny scrolls only in the *vibex* group (where the aedeagus sports a unique, midventral, caudally-directed prong).

The distal end of the uncus, which is divided, is bent farther dorsad in the *origenes* group (Figs. 1, 3, 5) than in any other group of *Polites*.

Female genitalia in *Polites* present less of a generic gestalt, varying more both within and between groups—and, to some degree, in parallel—so that group characterization is not as simple. In the *origenes* group (also in the *vibex* group, but in no others) the apophyses anteriores join the lamella postvaginalis via continuously sclerotized bands (Figs. 6–9). In the *origenes* group (also in *P. baracoa*) sclerotization of the lamella postvaginalis is intermediate (*P. puxillius* [Figs. 6, 7], *P. pupillus* [Figs. 8, 9], and *P. origenes*) to extensive (superspecies *P. mystic*) rather than limited (as it is in the *themistocles* group [MacNeill 1993] and in the *vibex* group [where the lamella postvaginalis carries a unique, midventral, short, sclerotized, finely spined keel]). In the *origenes* group sclerotization of the ductus bursae is partial and posterior; but it may be ventral only (superspecies *P. mystic*), ventral and lateral (*P. pupillus* [Figs. 8, 9]), or ventral, lateral, and, in a very narrow band, dorsal (*P. puxillius* [Figs. 6, 7], *P. origenes*, and, at times, vaguely, *P. pupillus*)—always with a longitudinal, midventral groove (Figs. 6–9) or break in the sclerotization. (Sclerotization of the ductus bursae is partial, posterior, but 360° and broadly ringlike [though midventrally weak] in the *vibex* group; partial, lengthy, mostly ventral but also somewhat lateral [resembling a long, essentially ungrooved, scoop] in *P. baracoa*; and complete, extending more or less the entire length of the ductus bursae and running all the way around, usually with a strong middorsal groove and a ventral pouch, in the *themistocles* group [MacNeill 1993].)

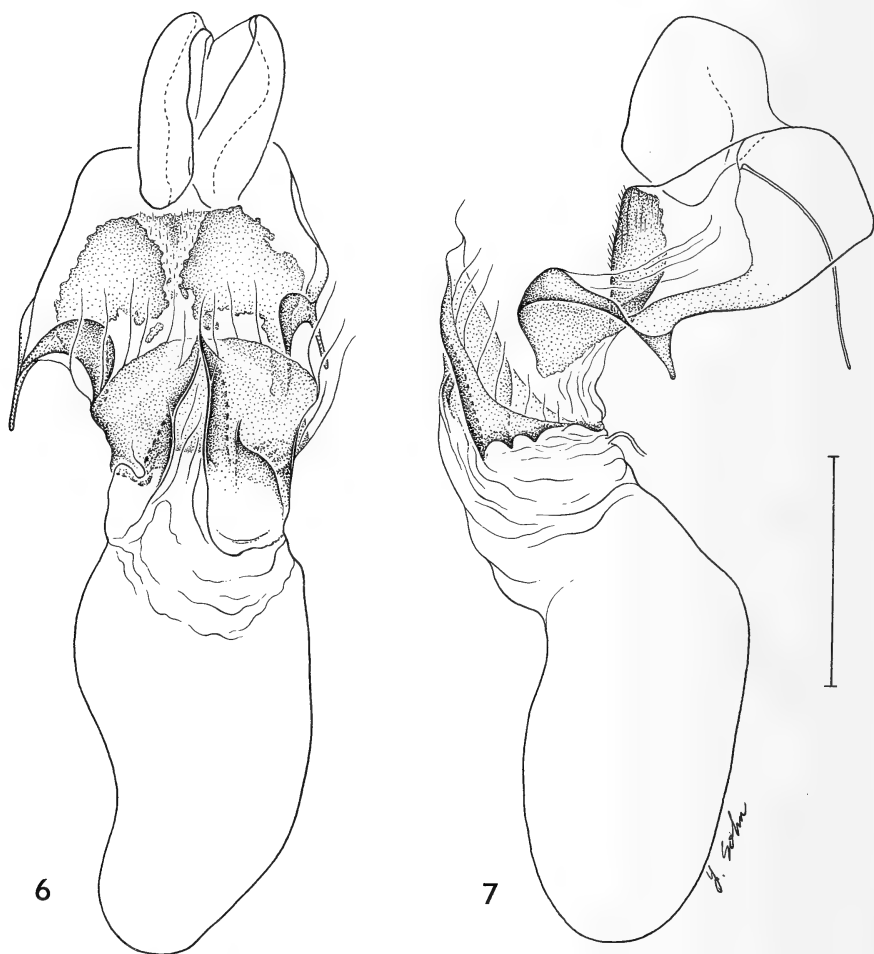
While the northern major differentiates of the *origenes* group of *Polites* (*P. origenes* and superspecies *P. mystic*) are widely known, repeatedly shown in the rising tide of North American butterfly books, and readily separable superficially, the southern differentiates (*P. puxillius* and *P. pupillus*) are not and must be treated here. Whereas in both sexes of *mystic* and *sonora* and in males of *origenes* extensive yellow to yellow-orange brightens the dorsal wing surface, in females of *origenes* and in both sexes of *puxillius* (Figs. 23, 24) and *pupillus* (Figs. 25, 26) the wings above look basically brown (with a variable set of small, pale spots [yellowish in *origenes*, white in *puxillius* and *pupillus*]). Wingshape is sexually dimorphic in the northern three species but not in the southern two: in *mystic*, *sonora*, and *origenes* the wings of males are narrower and more pointed, those of females, broader and

rounder; but in *puxillius* and *pupillus* the wings are broad and round in both sexes (Figs. 23–26). So, with respect to both color and wingshape, *puxillius* and *pupillus* tend to resemble females of *origenes*.

In the two Mexican species, wing spots, which are white, are expressed better by *pupillus* (Figs. 25, 26) than by *puxillius* (Figs. 23, 24). Forewing spots of *pupillus* look whiter and brighter partly because, in some to most of them, some scales stand up from the surface of the wing so as to let light through. In *puxillius* all the white scales lie flat against the wing so that all spots are opaque, none hyaline. Usually, *pupillus* develops a full set of forewing spots—in spaces 1b, 2, 3, 4, 5, 6, 7, 8, and the cell (Figs. 25, 26)—but *puxillius* rarely does, almost always dropping the one or two spots in space 1b (Figs. 23, 24), often skipping those in spaces 4 and 5, as well as that in 8 (Fig. 23), and, in one male examined, losing all but spots 3 and 6. At least some hindwing spots (which are opaque) appear dorsally in *pupillus* (usually spots 2 to 6) (Figs. 25, 26) while none really do in *puxillius* (Fig. 23) (at most, there may be a suggestion of a spot in space 3—see Fig. 24). Ventrally, where spot development is better, up to a full set may surface in *pupillus*—in spaces 1c, 2, 3, 4, 5, 6, 7 (rare) and the cell (Figs. 25, 26); in *puxillius* ventral expression runs the gamut from all except the rare spot 7 (Fig. 24) to nothing whatsoever.

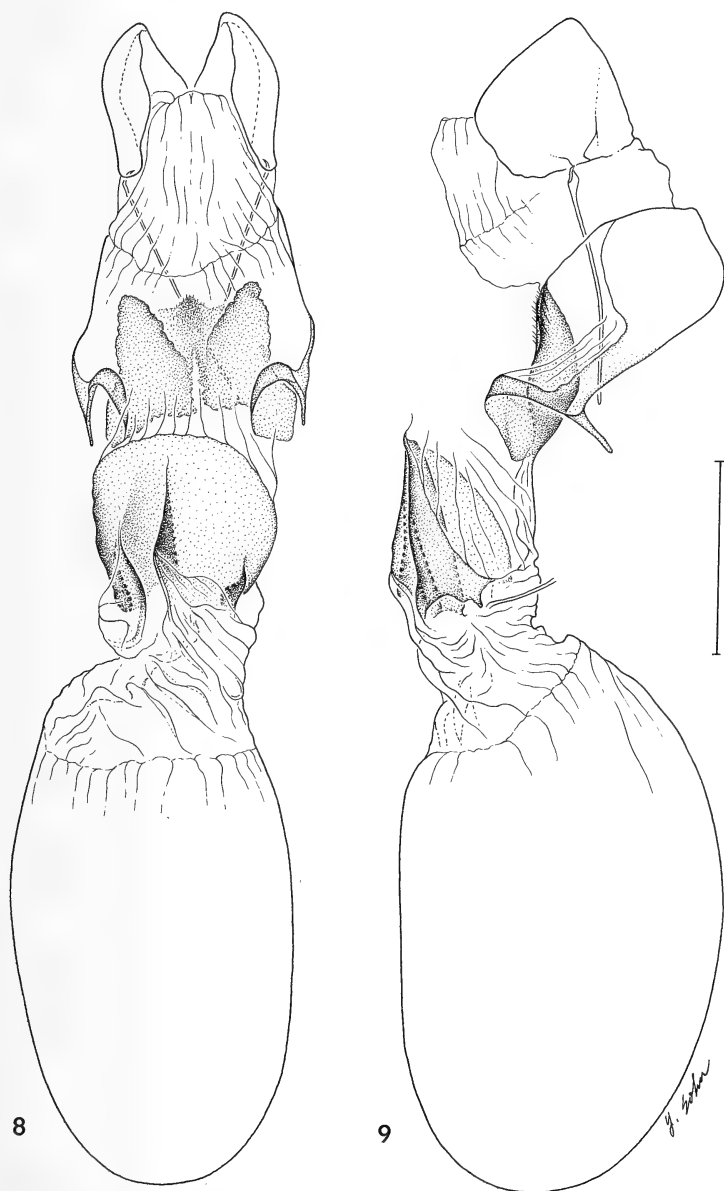
As for real interspecific differences in the conservative but individually variable male genitalia, titillator teeth are fewer in *puxillius* (Figs. 1–3), varying from 4 to 6 (usually 4) on each of the paired titillators, and commoner in *pupillus* (Figs. 4, 5), where they vary from 6 to 10 (usually 7 or 8). The valva of *puxillius*, in lateral view (Fig. 3), is more tapered distally along its ventral margin and hence not as broad (from top to bottom) at its distal end as it is in *pupillus* (Fig. 5). (Evans does not mention these differences; yet once you know what to look for, you can detect both of them in his [1955:pl. 78, M.21.1, M.21.2] genitalic cartoons.) In posterior view, the lower part of the divided distal end of the valva usually forms more of a U in *puxillius* (Fig. 2) than it does in *pupillus* (Fig. 4). Though conspicuous in the specimens figured, this difference almost vanishes when certain variants are compared. The greater valval height of *pupillus*, evident in lateral view, usually shows too in posterior view as a ventral, vertical extension below the U (compare Fig. 4 with Fig. 2).

One interspecific difference in the highly variable female genitalia crept into the foregoing group comparisons: the incomplete sclerotization of the ductus bursae (mainly ventral and lateral) continues dorsally to form a narrow but unmistakable sclerotized ring around the ductus in *puxillius* (Figs. 6, 7) but not—or, at best, very weakly—in *pupillus* (Figs. 8, 9). In addition, the sides of the midventral groove in



FIGS. 6, 7. Female genitalia of *Polites puxillius* from 25 mi (40 km) W Durango, Durango, MEXICO, 5 August 1972, MacNeill & Viers [X-2653] (USNM). Scale = 1.0 mm. **6**, Ovipositor lobes (retracted), eighth tergite with apophyses anteriores (sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **7**, The same, plus the right apophysis posterioris and part of the ductus seminalis, in right lateral view.

the ductal sclerotization are more divergent anteriorly in *puxillius* (Fig. 6) than in *pupillus* (Fig. 8), and the sclerotization itself is more fluted in *puxillius* (Figs. 6, 7) than it is in *pupillus* (Figs. 8, 9). The lateral part of the ductal sclerotization (which is more extensive on the left side than on the right—see Figs. 7, 9) is more extensive on both sides in *pupillus* than it is in *puxillius*; so it better hides the roof of the



FIGS. 8, 9. Female genitalia of *Polites pupillus* from 34 mi (55 km) SE Acatlán, 6000 ft (1830 m), Puebla, MEXICO, 9 July 1952, E. E. Gilbert, C. D. MacNeill [X-3198] (MacNeill collection). Scale = 1.0 mm. **8**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **9**, The same, plus part of the ductus seminais, in right lateral view.



midventral groove in lateral view in *pupillus* (Fig. 9) than in *puxillius* (Fig. 7). Again in lateral view, the roof of the midventral groove is convex in *puxillius* (Fig. 7) but straight in *pupillus* (Fig. 9). All these interspecific differences are rather subtle.

*Polites pupillus* is larger than *P. puxillius*. In each species the forewing of the female averages about one mm longer than that of the male, and in each sex the forewing of *pupillus* averages about one mm longer than that of *puxillius*:

	sex	mean	range	n
<i>puxillius</i>	♂	13.6	12.6–14.4	9
	♀	14.9	14.0–15.6	13
<i>pupillus</i>	♂	14.8	13.5–16.2	16
	♀	15.7	15.0–16.4	5

The number of segments in the nudum of the antenna ranges from 11 to 13 in *puxillius* (mean = 12.2, n = 21) and from 11 to 14 in *pupillus* (mean = 12.8, n = 20). In both species nudum segments are evenly split between the body of the club and the apiculus.

Although both species are montane, *P. puxillius* is higher, altitudinally tighter (recorded from 8000 to 8500 ft [2440–2590 m]), and less widely distributed (Durango [Fig. 10]—to as far south as Guerrero according to Godman 1900, Hoffmann 1941). *Polites pupillus* extends from 4200 to 7500 ft (1280–2285 m) and from Sonora and Sinaloa to Colima, Puebla, Guerrero, and Oaxaca (Fig. 10). So far as known, flight times are similar: dates on specimens of *puxillius* examined run from 18 July to 11 August; on *pupillus*, from 3 July to 8 August.

#### THE RHESUS GROUP OF *POLITES*

The *rhesus* group of *Polites* comprises at least three species (usually treated as two) that collectively range from the grasslands of southern Saskatchewan and Alberta, Canada, through the western Great Plains, southern Rocky Mountains, and southwestern United States, through Mexico and Central America, to the middle of Panama. Although Godman (1900:474) noted that “the structure of the genitalia of the males is very similar in the two species” when he put them in his new genus *Chaerephon*, he did not see the great similarity between their genitalia (Godman 1900:pl. 93, figs. 4 and 7—my Figs. 15, 16) and those of what he called *Thymelicus vibex* (pl. 93, fig. 14) and *Poanopsis puxillius* (pl. 93, fig. 40—my Fig. 1), which were on the same plate and which now are both in *Polites*. Likewise, Skinner and Williams (1923) figured the

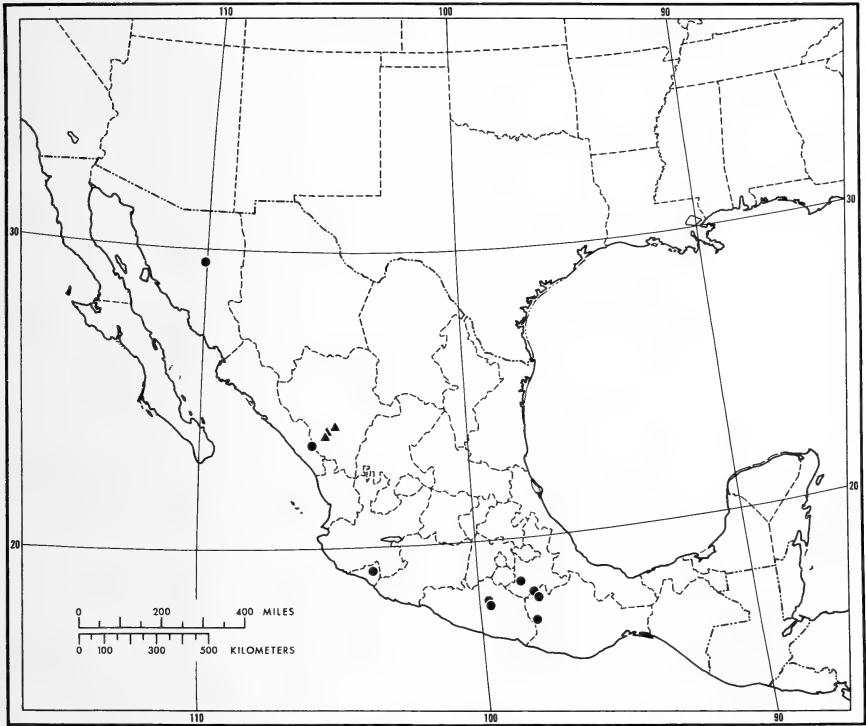
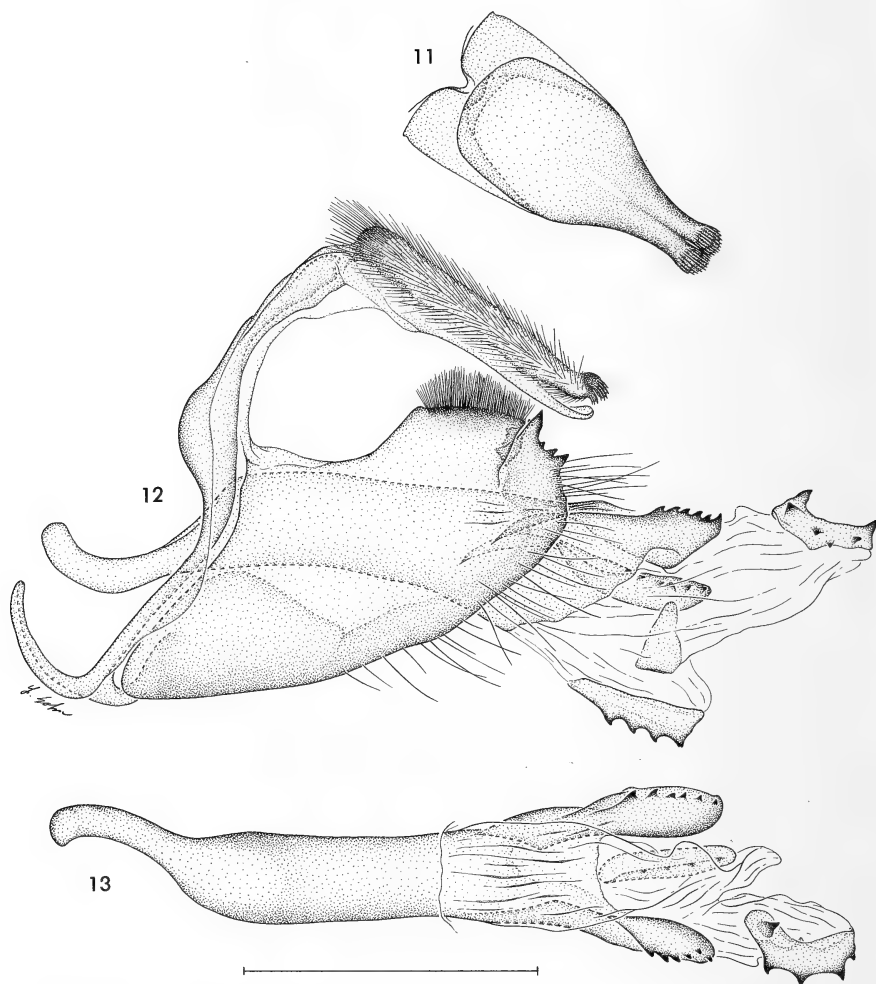


FIG. 10. Geographic distribution (based on plottable material examined) of Mexican sister species *Polites puxillus* (triangles) and *P. pupillus* (dots).

male genitalia of the two U.S. species of *Chaerephon* and then (1924) those of nine U.S. species of *Polites* without seeing how remarkably close they are. Enamored of names, Hemming (1935) saw that *Chaerephon* Godman is a junior homonym and replaced it with *Yvretta*. Commenting that its “genitalia [are] very like those of *Polites*,” Evans (1955:315) still set *Yvretta* next to *Hylephila*, six genera removed from *Polites* (and 21 genera from *Poanopsis*). MacNeill (1993:177) observed that “male genitalic similarities suggest that the nearest relatives of *Polites* are the genera *Yvretta* Hemming, *Hylephila* Billberg, and *Wallengrenia* Berg.” I am going much further by reducing *Yvretta* to a new species group of *Polites*, with the species *Polites rhesus* (Edwards), *P. carus* (Edwards), and *P. subreticulata* (Plötz) (**new combinations**).

Like all other elements of the male genitalia, the aedeagus in the *rhesus* group has that *Polites* look: anteriorly narrow, it at least doubles in size (in lateral view) with the entry of the ductus ejaculatorius and more or less flares at the elaborate distal end, which flaunts a pair of



FIGS. 11–13. Male genitalia of *Polites subreticulata* from Coatepec, Veracruz, MEXICO, October 1910, R. Müller [X-3499] (USNM). Scale = 1.0 mm. **11**, Tegumen and uncus (gnathos hidden) in dorsal view; **12**, Complete genitalia (minus right valva and juxta) in left lateral view (left titillator more dorsal and more tightly dentate than right), with vesica everted showing all three cornuti (two dentate [upper one curved, lower one straight] and one without teeth); this individual somewhat malformed anteriorly: saccus curved sharply upward, aedeagus bent to right, and bottom of tegumen not curved ventrad near juncture with vinculum (compare Fig. 14); **13**, Aedeagus in dorsal view (left titillator more tightly dentate than right), with vesica everted (only the two dentate cornuti visible).

toothed titillators as well as toothed cornuti in the vesica (Figs. 1, 3, 5, 12–16, and figs. 11–19 in MacNeill 1993).

In the *rhesus* group, the paired, toothed titillators come from the upper part of the distal end of the aedeagus, extend backward with

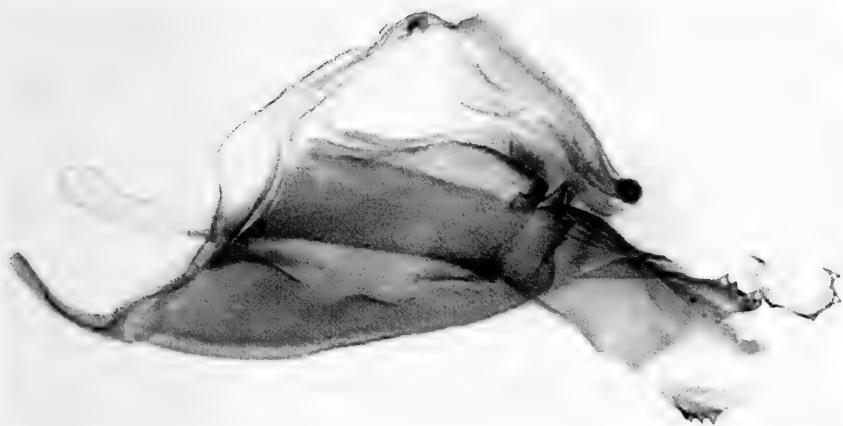


FIG. 14. Male genitalia (digital image) of *Polites rhesus* from Sapillo Creek Valley, 5800 ft (1770 m), 12 mi (19 km) N Pinos Altos, Grant Co., New Mexico, USA, 28 May 1959, J. M. & S. N. Burns [X-2712] (USNM). Complete genitalia in left lateral view (right titillator out of focus and toothless cornutus hidden), with vesica everted showing both dentate cornuti (upper one curved, lower one straight).

one twist along their narrow length, and then expand distally into the dentate portion, with 3 to 7 teeth (usually 5) on the left titillator and 4 to 7 teeth (usually 4, 5, or 6) on the right (Figs. 12–16). The teeth are closer together on the left titillator than they are on the right one (Figs. 12, 13). In another asymmetric touch, the left titillator is more dorsal than the right one (Fig. 12). Like the number of teeth, the length of the titillators varies individually instead of interspecifically or geographically: in each species of the *rhesus* group, the titillators may be equal (Figs. 12, 13, 15), or the left one may be a little to a lot shorter than the right. Two of the three cornuti are conspicuous and tentlike—one essentially straight, the other slightly to very curved, each with 3 to 6 teeth, which are closer together on the straight cornutus than they are on the curved one (Figs. 12–14). The third cornutus is very inconspicuous, amounting to nothing but a bit of lightly sclerotized vesica (Fig. 12).

Right down to the titillators and cornuti, the aedeagus of the *rhesus* group recalls that of the *themistocles* group (compare Figs. 12–16 with figs. 11–19 in MacNeill 1993 and see MacNeill's diagnosis of the *themistocles* group). Some variation is less rampant in the *themistocles* group, even though that group is larger: in *P. themistocles* (Latreille) itself, the two titillators are always the same length (fig. 19 in MacNeill 1993); and in what I consider the *peckius* subgroup comprising *P. peckius* (Kirby), *P. sabuleti* (Boisduval), *P. norae* MacNeill, *P. draco* (Edwards), and *P. mardon* (Edwards), the left titillator is always much shorter



FIGS. 15, 16. Male genitalia of *rhesus* group *Polites* (minus left valva) in left lateral view (ex Godman 1900:pl. 93, figs. 4, 7). **15**, *Polites subreticulata* from MEXICO or GUATEMALA (aedeagus artificially rotated so that the left titillator is lower than the right whereas the reverse is really true); **16**, *Polites rhesus* from Milpas, 5900 ft (1800 m), Durango, MEXICO (tegumen plus uncus artificially twisted so that the underlying gnathos and the gap between it and the uncus fail to show).

than the right (figs. 11–18 in MacNeill 1993). Throughout the *themistocles* group, the third, lightly sclerotized cornutus (inconspicuous in the *rhesus* group) is elongate and suggestive of a scouring pad (with a surface that MacNeill [1993] calls “minutely scobinate”). Otherwise, the basic forms and arrangements of aedeagal accessories are closely similar in the *rhesus* and *themistocles* groups (small differences will be evident in the comparison of figures—but a few figures cannot adequately convey individual variation, which tends to weaken such differences). In contrast, forms and arrangements of aedeagal accessories differ sharply (and in different ways) in the *origenes* group (Figs. 1–5), the *vibex* group, and *P. baracoa*.

What aspects of the male genitalia set the *rhesus* group apart? In *Polites* the distal end of the uncus is divided: each of the two uncal tips terminates in a two-layered comb, with extremely close-set tines curving backward and downward in each layer. These “uncal combs” (called “pectines” by MacNeill 1993) are slightly enlarged in the *rhesus* group (Figs. 11, 12, 14, 16), intermediate in the *themistocles* and *origenes* (Figs. 2–5) groups, reduced in the *vibex* group, and absent in *P. baracoa*. There is a sizable gap between the distal end of the uncus and the underlying divided gnathos in the *rhesus* (Figs. 12, 14, 15), *origenes* (Figs. 1, 3, 5), and *vibex* groups, and in *P. themistocles* (fig. 10 in MacNeill 1993)—but not in other members of the *themistocles* group (i.e., the *peckius* subgroup), where the gnathos is up against the bottom of the uncus (figs. 2–9 in MacNeill 1993). There is no gap in *P. baracoa*, either, but for a totally different reason: this species has lost the underlying divided gnathos.

In *Polites* the dorsodistal corner of the valva is split by a small notch (Figs. 3, 5, 12, 14–16, and figs. 2–10 in MacNeill 1993): the dorsal margin of the valva immediately anterior to this notch supports a dense field of more or less dorsally-directed bristles; and the posterior margin of the valva immediately posterior to this notch displays (in lateral view) at least one sizable, dorsally- or dorsocaudally-directed tooth

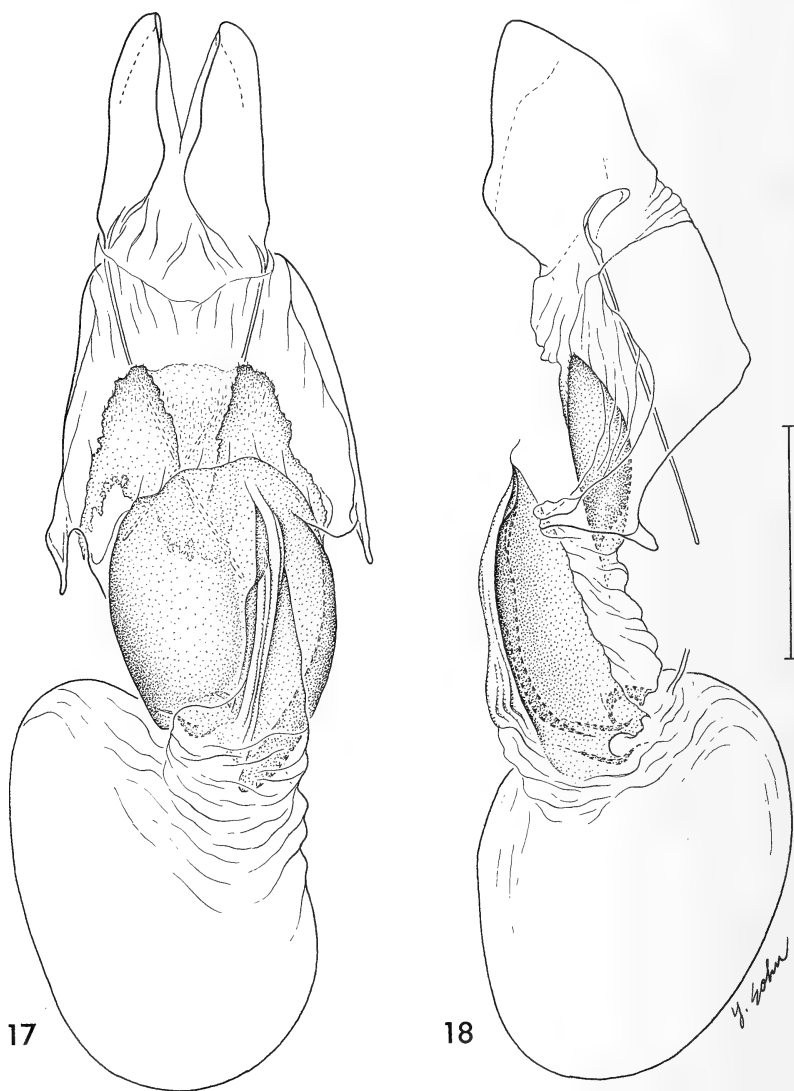
which, in turn, joins one or more teeth (readily visible in posterior view [Figs. 2, 4]) that extend mediad beneath the more or less medially-expanded posterior edge of the dense field of bristles. Medial expansion of the bristled area is least in the *vibex* and *themistocles* groups, strong in the *origenes* group, and greatest in *P. baracoa* and the *rhesus* group. In lateral view this expansion produces a slight hump (in the *origenes* group, Figs. 3, 5) to a very perceptible hump (in *P. baracoa* and the *rhesus* group, Figs. 12, 14) on the dorsal margin of the valva anterior to the valval notch. The posterior edge of the dense field of bristles is without teeth in the *rhesus* group, finely dentate in the *themistocles* group, more coarsely dentate in *P. baracoa* and the *origenes* group (Figs. 2, 4), and most coarsely dentate in the *vibex* group.

About halfway down the posterior margin of the valva (in lateral view) a massive projection extends backward in *P. baracoa* and one or more sizable teeth point backward in the *rhesus* group (Figs. 12, 14–16). This portion of the posterior margin is finely dentate (Figs. 3, 5) to smooth in the *origenes* group and essentially smooth in the *vibex* and *themistocles* groups (figs. 2–10 in MacNeill 1993).

The one or more teeth—visible in posterior view (Figs. 2, 4)—that extend mediad beneath the posterior edge of the dense field of bristles, are conspicuously multiple in the *origenes* group (Figs. 2, 4), in the *vibex* group, in *P. baracoa*, and in *P. themistocles* but are single to inconspicuously multiple especially in the *peckius* subgroup but also, somewhat less consistently, in the *rhesus* group.

The posterior margin of the valva (in lateral view) has more of a “chin”—so looks more squared off—in the *rhesus* group (Figs. 12, 14–16) than in any other group of *Polites*. Certain members of the *origenes* group (*P. mystic*, *P. sonora*, *P. pupillus* [Fig. 5], and some individuals of *P. origenes*) come closest to this well-chinned look. Farthest from it, in a sense, is the *vibex* group because the posterior half of the ventral margin of the valva is narrowly excised.

Female genitalia in the *rhesus* group (Figs. 17–22) are broadly reminiscent of those of the *origenes* group—particularly *P. origenes*, *P. puxillius*, and *P. pupillus* (Figs. 6–9)—except that the apophyses anteriores are not sclerotically connected to the lamella postvaginalis. Sclerotization of the lamella postvaginalis is intermediate, as in *P. origenes*, *P. puxillius*, and *P. pupillus*. Sclerotization of the ductus bursae is partial—mostly ventral and lateral, with a narrow, dorsal extension anteriorly—in *P. rhesus* (Figs. 17, 18) and *P. carus* (Figs. 19, 20), much as in *P. origenes*, *P. puxillius* (Figs. 6, 7), and *P. pupillus* (Figs. 8, 9); but it is virtually complete in *P. subreticulata* (Figs. 21, 22). In all three species of the *rhesus* group, as in all members of the *origenes* group, the ductus bursae has a ventral, longitudinal groove or break. This



FIGS. 17, 18. Female genitalia of *Polites rhesus* from Denver, Colorado, USA [X-3490] (USNM). Scale = 1.0 mm. **17**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (not sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **18**, The same, plus part of the ductus seminalis, in right lateral view.

groove is to the right of center in the *rhesus* group (Figs. 17, 19; 21) instead of more or less midventral as it is in the *origenes* group (Figs. 6, 8).

Owing to their overall conservatism and their individual variation,



the male genitalia of the *rhesus* group are not diagnostic at the specific level. But here, as in the *themistocles* group, external color pattern separates species: the underside of the hindwing instantly sets *P. rhesus* (Figs. 27, 28) apart from *P. carus* (Figs. 29, 30) and *P. subreticulata* (Figs. 31, 32). These last two species are much more similar in pattern (so much so that they are mistakenly regarded as subspecies). Color may help in determining unworn specimens: the spots of the upperside are usually creamy to pale yellow in *P. carus* and light to medium yellow-orange in *P. subreticulata*. Although the undersides tend to be creamier in *carus*, yellower in *subreticulata*, they overlap considerably.

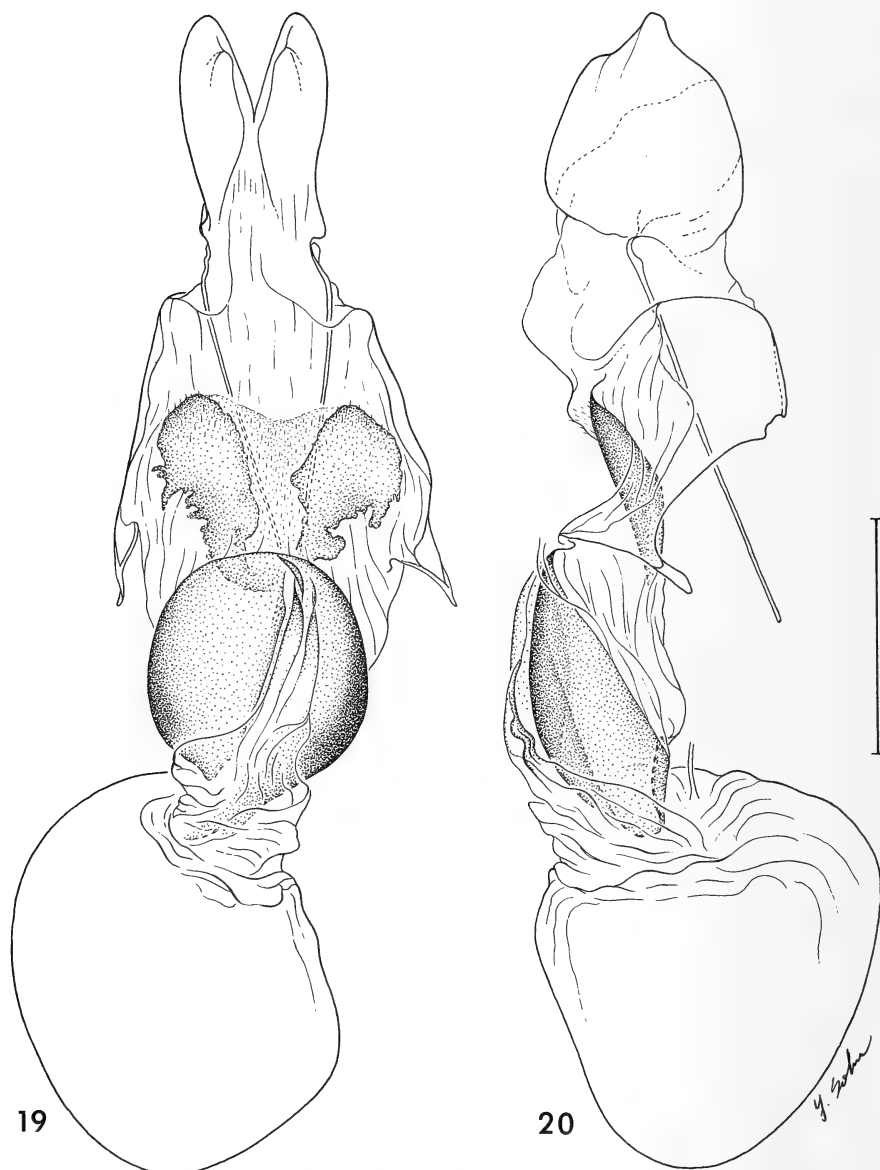
It is the female genitalia that best distinguish these species. The ductus bursae is only about half sclerotized (ventrally and laterally) in *P. carus* (Figs. 19, 20) but almost fully sclerotized in *P. subreticulata* (Figs. 21, 22). In both, the sclerotized ductus bursae usually looks rather globular in ventral view (Figs. 19, 21); but in *P. subreticulata* it tends—dorso-laterally—to extend backward slightly (and usually to flare slightly) at the ostium bursae (Fig. 21). Genitalic differences between *P. carus* and the superficially distinct *P. rhesus* are much more subtle because in *rhesus*, as in *carus*, the ductus bursae is only about half sclerotized (ventrally and laterally) (Figs. 17, 18). However, the sclerotized ductus bursae looks a little more elongate in *P. rhesus*, especially in ventral view (Fig. 17); and, where it approaches the corpus bursae, the anterior edge of the sclerotization is more irregular in *rhesus* (Fig. 18) than it is in *P. carus* (Fig. 20) (and, for that matter, *P. subreticulata* [Fig. 22]).

*Polites rhesus* ranges from southern Canada (Saskatchewan and Alberta), in a fairly narrow strip through the western Great Plains and southern Rocky Mountains of the United States (Stanford & Opler 1993), to high mountains of central Mexico (10,000 ft [3050 m] in the state of México); *P. carus*, from the southwestern United States (western Texas to southeastern California—see Stanford & Opler 1993) to central Mexico (Distrito Federal); and *P. subreticulata*, from central Mexico (Sinaloa, Jalisco, Colima, Michoacán, Distrito Federal, Morelos, and Veracruz), through Central America, to Panama (as far, at least, as the Canal).

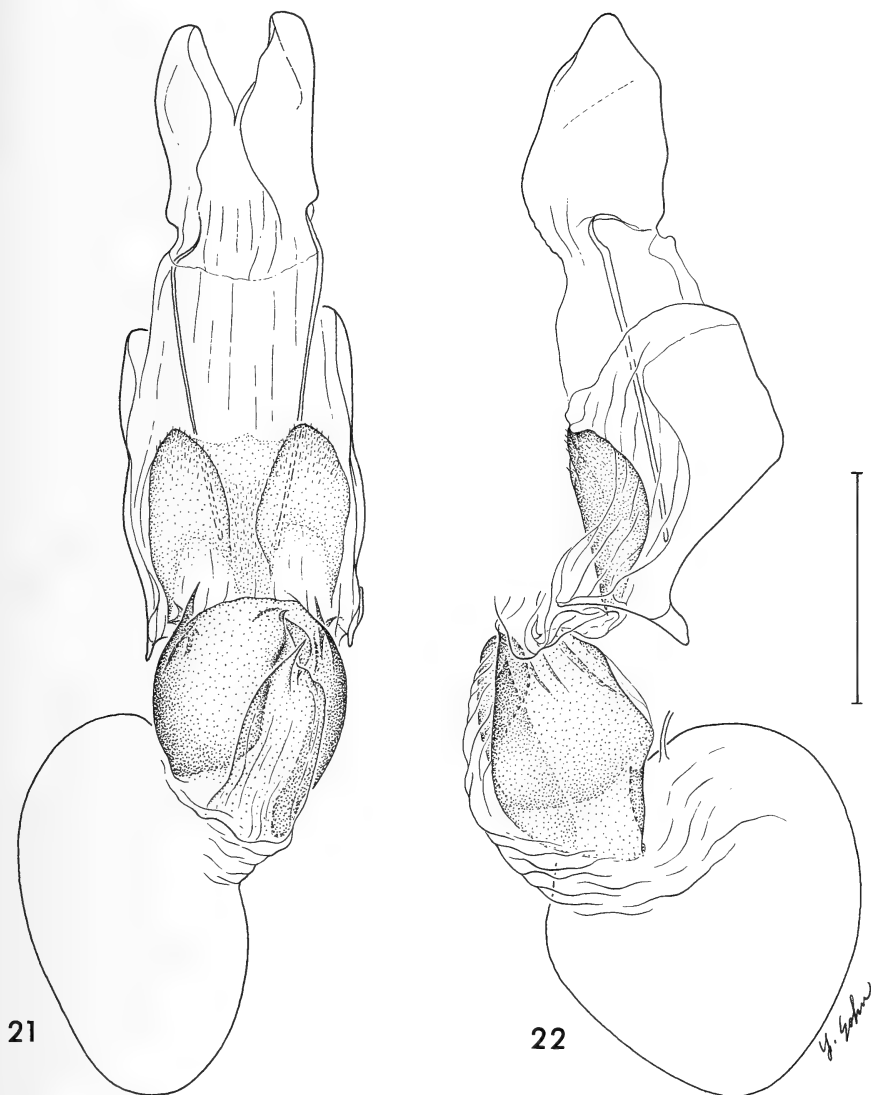
## DISCUSSION

### Generic Limits and Vanishing Traits

Extending generic limits this way calls for more discussion of variation in characters—especially their reduction and loss. The form of the antennal club and the length of its reflexed apiculus, which are widely used in skipper classification, are undeniably valuable. However, though they tend to be conservative at the generic level, they are hardly im-



FIGS. 19, 20. Female genitalia of *Polites carus* from Sunny Glen Ranch, 5000–7000 ft (1525–2135 m), near Alpine, Texas, USA, 1–15 May 1926 [X-3488] (USNM). Scale = 1.0 mm. **19**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (not sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **20**, The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 21, 22. Female genitalia of *Polites subreticulata* from Mazatlán, Sinaloa, MEXICO, J. A. Kusche [X-3494] (USNM). Scale = 1.0 mm. **21**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (not sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **22**, The same, plus part of the ductus seminalis, in right lateral view.



23



24



25



26



27



28



29



30



31



32

FIGS. 23–32. Adults of species moved to *Polites* (all  $\times 1$ ) (in USNM unless otherwise indicated); in each figure, upperside on left, underside on right. **23**, *puxillius*  $\delta$ , 28 mi (45 km) E El Salto, 8400 ft (2560 m), Durango, MEXICO, 6–7 August 1972, Vairs & MacNeill (MacNeill collection); **24**, *puxillius*  $\eta$ , 25 mi (40 km) W Durango, 8100 ft (2470 m), Durango, MEXICO, 20 July 1964, J. A. Chemsak [X-3196] (Univ. Calif. Berkeley collection); **25**, *pupillus*  $\delta$ , Sierra de Guerrero, MEXICO, July 1913, R. Müller [X-2699] (type of *Amblyscirtes catahorma* Dyar); **26**, *pupillus*  $\eta$ , 2 mi (3 km) SW Potrerillos, 4200 ft (1280 m), Sinaloa, MEXICO, 7–8 August 1986, J. Brown & Powell [X-3203] (Univ. Calif. Berkeley collection); **27**, *rhesus*  $\delta$ , Sapillo Creek Valley, 5800 ft (1770 m), 12 mi (19 km) N Pinos Altos, Grant Co., New Mexico, USA, 28 May 1959, J. M. & S. N. Burns [X-2712]; **28**, *rhesus*  $\eta$ , Cedar Creek Canyon, 6900 ft (2100 m), Ruidoso, Lincoln Co., New Mexico, USA, 24 May 1959, J. M. & S. N. Burns [X-3504]; **29**, *carus*  $\delta$ , Portal, Chiricahua Mountains, 4800 ft (1465 m), Cochise Co., Arizona, USA, 18 July 1974, J. M. & S. N. Burns [X-2708]; **30**, *carus*  $\eta$ , 6.5 mi (10.5 km) NE Sawtooth Mountain, Davis Mountains, 5600 ft (1705 m), Jeff Davis Co., Texas, USA, 28 April 1959, J. M. & S. N. Burns; **31**, *subreticulata*  $\delta$ , Mexico City, MEXICO, 7 June 1897, O. W. Barrett [X-3498] (forewing with a long tear in space 1b); **32**, *subreticulata*  $\eta$ , Mexico City, MEXICO [X-3491].

mutable. For example, *Amblyscirtes alternata* (Grote & Robinson), which is an *Amblyscirtes* in the narrowest sense, is unique among all those species in having the sizable, delicate, sharp apiculus suddenly reduced to a short, blunt fraction of itself (Burns 1990). Lumping *Yvretta* with *Polites* may bother those who overweigh antennal clubs because the very short but definite apiculus of the rest of *Polites* seems to be lacking in the *rhesus* group. (Its blunt antennal club is one of the main reasons why *Yvretta* was created in the first place and kept well removed from *Polites*.) But in most specimens of each of the species of the *rhesus* group the blunt club actually ends in a slightly reflexed nubbin (comprising a few segments) that looks like a variably vestigial apiculus. A supposedly important difference between the *rhesus* group and the rest of *Polites* becomes relatively trivial.

Differences in stigmal expression are demonstrably insignificant. Although males of *P. carus* and *P. subreticulata* of the *rhesus* group have a fairly well developed, *Polites*-type stigma, males of *P. rhesus* do not: the stigma is, at best, variably vestigial, and is usually missing altogether. In apparent contrast, "real" *Polites* males "always" develop a good stigma—or they did until MacNeill (1993) described *P. norae*, which produces nothing at all. (*Polites norae* is near *P. sabuleti* in the stigmally well endowed *themistocles* group.) Stigmal expression has been shown to vary in a similar, unpredictable manner within other genera. Despite a respectable male stigma in most species of *Atrytonopsis*, the *lunus* group entirely lacks one (Burns 1982), and *A. deva* (Edwards) "runs a gamut from no stigma, through many and various vestigial and reduced expressions, all the way to the complete three-part structure" (Burns 1982:551).

On the genitalic front, no importance can be attached to the fact that the uncal combs of the *rhesus* group are bigger than those of other *Polites*. They are only about as much larger than those of the *themistocles* and *origenes* groups as those of the *vibex* group are smaller. At the farthest extreme, *Polites* includes *baracoa*, whose uncal combs have vanished without a trace. Moreover, *baracoa* has lost its gnathos. And, in a different kind of unique development, its paired, toothed, caudally-extending titillators have broadly joined each other, near their anterior ends, across the underside of the aedeagus. Altogether, in its genitalic morphology, the *rhesus* group is considerably closer to the *Polites* mainstream than is *P. baracoa*.

Some may be jolted by the broad, round, female-like wings of males of *P. puxillus* (Fig. 23) and *P. pupillus* (Fig. 25) within the *origenes* group, where males of all other species have narrower, more pointed wings than do females. But sexual dimorphism in wingshape (which is typical and extremely widespread in skippers) has abruptly disappeared

elsewhere within the genus *Polites*—in *P. mardon* within the *peckius* subgroup of the *themistocles* group.

### Distribution and Speciation

In the *origenes* group, *P. origenes* (mainly from the eastern and central United States) morphologically and geographically links the northern, transcontinental superspecies *P. mystic* (*P. mystic* and *P. sonora*) and the Mexican sister species *P. pupillus* and *P. puxillus*. These montane sisters appear to be closely allopatric, in part through different altitudinal preferences; but data are too few to say for sure (see Fig. 10). Phylogenetically closer to the Mexican sisters than to superspecies *P. mystic*, *P. origenes* is out of touch with them and broadly sympatric with the superspecies—mostly with *P. mystic* (see maps in Opler & Malikul 1992, Stanford & Opler 1993). However, across all five species of the group, sympatry is limited. Their spatial distribution strongly reflects a set of allopatric speciation events.

In the *rhesus* group, the superficially distinctive and more northward ranging *P. rhesus* extensively overlaps *P. carus* in the southwestern United States and northern Mexico, whereas *P. carus* and *P. subreticulata*, which are sister species, seem (from meager distributional data) almost to replace each other geographically.

Again, the four strictly western members of the *peckius* subgroup of the *themistocles* group—*P. draco*, *P. sabuleti*, *P. norae*, and *P. mardon*—are essentially allopatric (MacNeill 1993). So are several members of the *vibex* group, which Evans (1955) erroneously treated as a single, very widely distributed polytypic species.

All four species groups of *Polites* overlap in distribution, ranging in broadly repetitious—though different—patterns from the neotropics to the nearctic: the *vibex* group from Argentina, Paraguay, Brazil, Bolivia, and Peru to Mexico, the West Indies, and (primarily) the southeastern United States; the *rhesus* group from Panama to southern central Canada; the *origenes* group from southern Mexico to the width of southern Canada; and the *themistocles* group from central Mexico to the width of southern Canada, plus Yukon Territory. But all four species groups of *Polites* still give clear distributional evidence of allopatric speciation within themselves. This is independent evidence that the morphologically defined species groups are correct.

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some. Don Harvey helped with the map (Fig. 10). Elizabeth Klafter and the late Adrienne Venables dissected genitalia (126 KOH-preparations of *Polites*, about evenly split between the sexes). Daniel Otte at The Academy of Natural Sciences, Philadelphia, Pennsylvania, made a digital image of one dissection (Fig. 14), Victor E. Krantz photographed adults (Figs. 23–32) as well as the Godman genitalic illustrations (Figs. 1, 15, 16), and Young Sohn drew eight dissections (Figs. 2–9, 11–13, 17–22) and then mounted all figures. Sarah Burns aided in many ways. George T. Austin and C. Don MacNeill perused the manuscript. My thanks to everyone.

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A NEW SPECIES OF *ACROLEPIOPSIS* AND THE  
DESCRIPTION OF THE FEMALE OF  
*A. CALIFORNICA* (ACROLEPIIDAE)

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**ABSTRACT.** The family Acrolepiidae, of the superfamily Yponomeutoidea, includes three genera: *Digitivalva* Gaedike, *Acrolepiopsis* Gaedike, and *Acrolepia* Curtis. *Acrolepiopsis liliivora*, new species, from California and Oregon, is described herein; the male and female genitalia are illustrated. Adults have been reared from the bulbs of *Lilium washingtonianum*. The female of *A. californica*, previously unknown, also is described, and the genitalia are illustrated. The larvae are reported to feed on *Disporum hookeri*.

**Additional key words:** *Acrolepiopsis liliivora*, genitalia (male and female), *Lilium washingtonianum*, *Disporum hookeri*.

Acrolepiidae is a family in the superfamily Yponomeutoidea. It is represented in all zoogeographical regions and includes 84 described species in three genera: *Digitivalva* Gaedike (40 species), *Acrolepiopsis* Gaedike (35 species), and *Acrolepia* Curtis (9 species). In the Nearctic and Neotropical regions there are 15 described species, three in *Digitivalva*, ten in *Acrolepiopsis*, and two in *Acrolepia* (Gaedike 1984a, 1984b). Undoubtedly, more detailed study of each zoogeographical region will increase the number of known species.

The known life histories indicate that acrolepiid larvae are leaf-skeletonizers or miners of leaves, fruit, or bulbs of Asteraceae (*Digitivalva*), Dioscoriaceae and Liliaceae (*Acrolepiopsis*), and Solanaceae (*Acrolepia*). While examining acrolepiid from the western United States, I discovered a new species of *Acrolepiopsis* and the previously undescribed female of *A. californica*. These are described below.

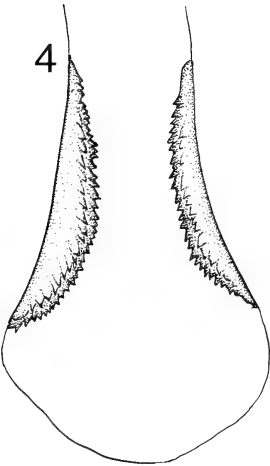
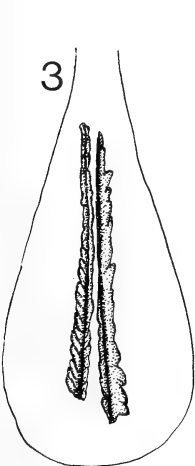
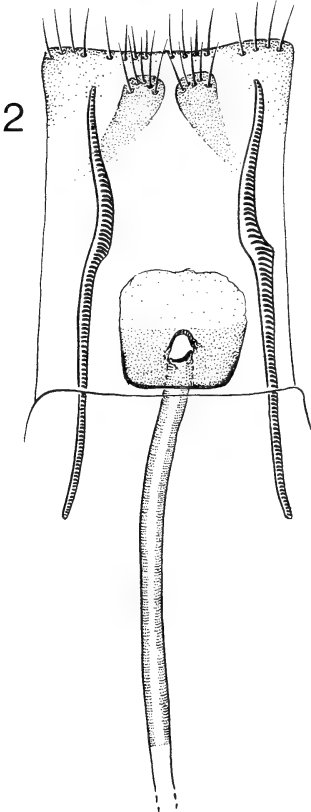
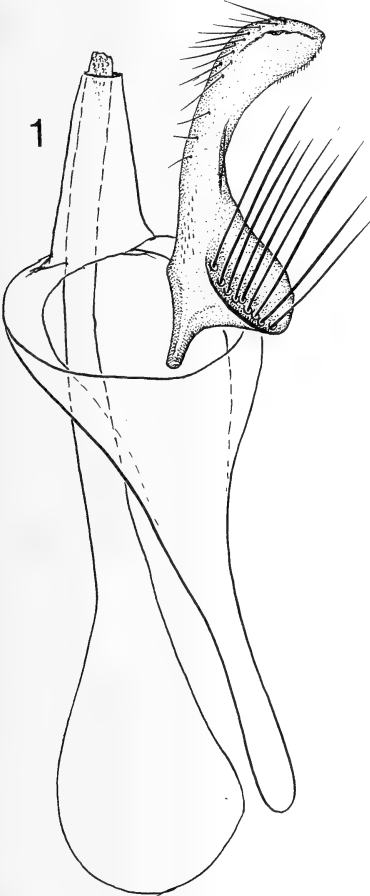
*Acrolepiopsis liliivora* Gaedike, new species

Wingspan 15–16 mm. Head dark brown, except vertex light brown; labial palpi dark brown. Thorax dark brown. Forewing dark brown, with white triangular spot, sometimes overlaid with dark scales, extending obliquely forward from margin of dorsum at  $\frac{1}{3}$  distance from base, with minute white dot on dorsum at base of cilia, and with individual light scales scattered throughout the dark area; cilia beneath apex pale distally. Males somewhat lighter brown than females. Male genitalia (Fig. 1): saccus elongate, narrow, apically rounded; valva with

→

FIGS. 1–4. Genitalia of *Acrolepiopsis liliivora* Gaedike, new species. 1, Male genitalia; 2, Female genitalia (sterigma); 3, Female genitalia (signa); 4, Female genitalia (signa).





base broad, narrowest medially and expanded apically, costal margin concave; aedeagus more than 2.5 times valva length, broad basally, tapering to apex, with minute sclerotizations in vesica. Female genitalia (Figs. 2-4): Eighth segment with a pair of relatively narrow, somewhat clublike structures bearing setae on the broadly rounded base; ostium with rectangular sclerotization, the lower half more strongly sclerotized; ductus bursae strongly sclerotized over most of its length; corpus bursae with two long signa; signa slightly bent with dentate inner surface, the appearance variable depending upon the preparation.

**Type locality:** California: Auto Rest. (I have been unable to determine the exact location.)

**Types:** Holotype male: Auto Rest, Cal.[ifornia] 18. 8. [19]18, on *Lilium washingtonianum*, Coll. David Griffiths (genital slide R. Gaedike No. 2421). Paratypes: 1 male, 3 females, same data as holotype; 1 female Oregon, Santiam Natl. For., reared from bulb of *Lilium washingtonianum*, emerged 9. X. 1931. The holotype and three paratypes are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; two paratypes are deposited in the Deutsches Entomologisches Institut (DEI) Eberswalde.

**Biology:** Larva in bulb of *Lilium washingtonianum* (Liliaceae), pupa in a net-like cocoon.

**Remarks:** All specimens are in poor condition. One female lacks forewings; another lacks a hindwing. The new species is closely related to *A. californica*. It differs in the coloration of the cilia below the apex, in having somewhat broader valvae and longer signa than *californica*.

### *Acrolepiopsis californica* Gaedike, 1984

Entomol. Abh. Staatl. Mus. Tierk. Dresden 47(1983)10:183-184, Fig. 20.

In material sent to me by J. Powell there were four specimens of this species, two of which were females. Because the female was previously unknown, I describe the female genitalia below.

**Female genitalia (Fig. 5):** The pair of ventrolateral clublike structures bearing setae on the broadly rounded base, tapering to a point; ostium with a somewhat cup-shaped sclerotization, the lower half more strongly sclerotized; ductus bursae strongly sclerotized; signa short, with dentate inner surface.

**Material examined:** Two males, two females, as follow: One male: Calif.: El Dorado Co., Blodgett Forest, 13 mi E Georgetown, 4000-4500', 27/28.V.1978, leg. J. Powell. One male: Calif.: Siskyou Co., McCloud River at Ash Creek Rgr. Sta., 9.VI.1974, leg. J. Powell. One female: Calif.: Myers Flat, Humboldt Co., 14.VIII.1963, leg. J. Powell. One female: Calif.: Big Creek Reserve (UCNLWR), Monterey Co., 26./

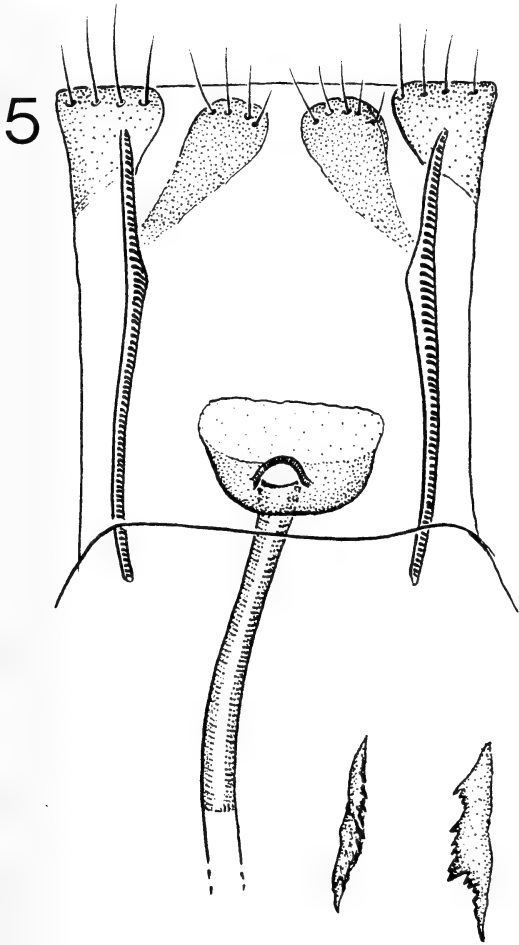


FIG. 5. Female genitalia of *Acrolepiopsis californica*.

28.V.1987, leg. J. Powell. These specimens are the first records of this species since its description.

**Biology:** J. Powell (*in litt.*) gives some remarks on the biology of this species: "... In late April [1990] I made additional collections of the larvae of *Acrolepiopsis* at Big Creek on *Disporum hookeri* and succeeded in rearing a few adults. This confirms the hostplant for the species represented by one specimen that I sent you from 1987. The larvae sometimes start to eating the inflorescence but sometimes do not; later they skeletonize the leaves, feeding on either upper or lower surfaces."

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## A NEW SPECIES OF *LAPARA* (SPHINGIDAE) FROM SOUTHEASTERN UNITED STATES

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**ABSTRACT.** *Lapara phaeobrachycerous*, new species, is described and illustrated. The new species presently is known to occur in extreme eastern Louisiana and the state of Mississippi in the southeastern United States. The species can be distinguished from *Lapara coniferarum* (J. E. Smith) by its slightly smaller size, darker color, the presence of a single postcellular dash, narrower wings, shorter antennae, and different flight period.

**Additional key words:** endemism, hawkmoths, Louisiana, voltinism.

Hodges (1971) recorded two species of *Lapara* in North America north of Mexico: *Lapara bombycoides* Walker and *Lapara coniferarum* (J. E. Smith). He treated *Lapara halicarnie* (Strecker) as a synonym of *L. coniferarum*, and *Lapara pinea* Lintner as a synonym of *L. bombycoides*. In his review of *Lapara*, Riotte (1972) recognized *L. halicarnie* as distinct on the basis of features of the labial palpus, pretarsus structure, color, size, maculation, genitalia, and larvae. Riotte also questioned the synonymy of *L. pinea* with *L. bombycoides*. Previous authors (e.g., Holland 1903, Clark 1919), also noted or discussed the problems associated with the "hypertrophied" type specimen of *L. halicarnie*.

At the time of Riotte's (1972) review, no *Lapara* species were known from west of the Mississippi River in the United States, and none was known to occur in Louisiana. Riotte examined 241 examples of *L. coniferarum* from 13 states, mostly bordering the east and Gulf coast, from New York and Rhode Island southward to Florida and westward to Mississippi. He also examined 649 examples of *L. bombycoides* from a much greater range, 48 examples of *L. halicarnie* from four southeastern states, and the type of *L. pinea* from New York.

Since 1972, 8422 specimens of *Lapara* from Louisiana have been collected by the author using ultraviolet light traps. Most of the better quality specimens are pinned, spread, and labeled, and are in the author's collection. From 1972 through 1985, 1946 specimens were collected and recorded as *L. coniferarum*. From 1986 through 1992, specimens were segregated into two phenotypes. During these seven years, 6473 *Lapara* specimens were collected: 2247 (35%) are *L. phaeobrachycerous*, new species, and 4226 (65%) are *L. coniferarum*.

### *Lapara phaeobrachycerous* Brou, new species

(Figs. 1A & B)

**Male.** Head: Dark charcoal gray to occasional brownish gray in color, scales on front and vertex form a bluntly rounded area between an-

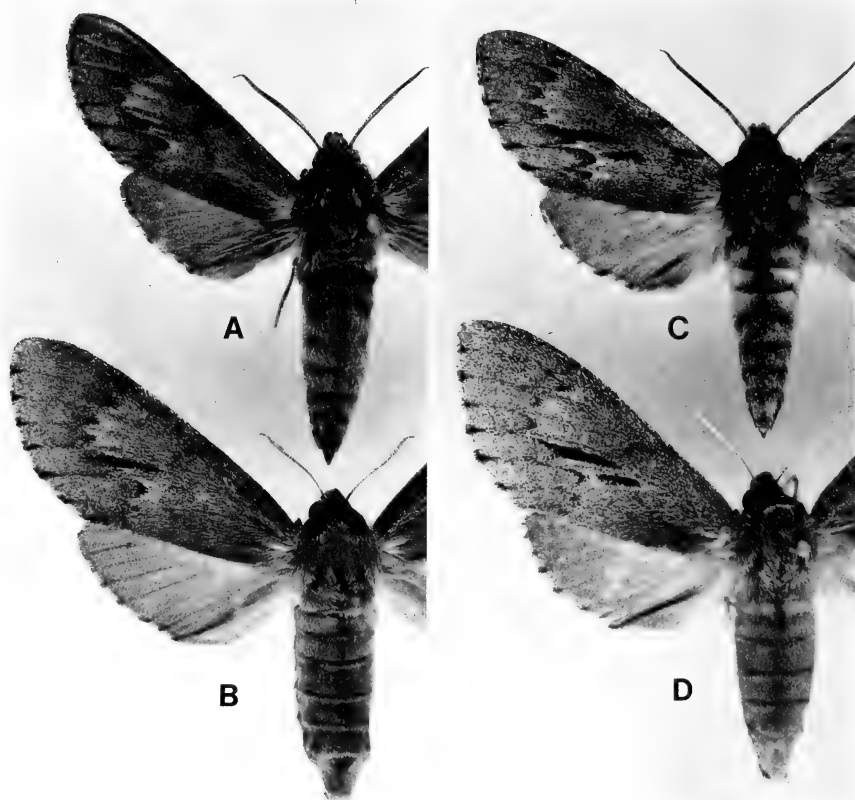


FIG. 1. The *Lapara* of Louisiana: *L. phaeobrachycerous*, A. male holotype, B. female allotype. *L. coniferarum*, C. male, D. female. Specimens pictured were collected at Louisiana, St. Tammany Parish, 6.8 km NE Abita Springs.

tennae. Antennae laminate, biciliate, weakly hooked tip, length  $\bar{x}$  = 10.3 mm (9.0–12.0;  $n$  = 40). Thorax: Color above as described for head, below a slightly lighter shade. Forewing: Dorsal color charcoal gray, whitish scales mostly limited to area basad along curving postmedial line, usually one prominent postcellular dash, though a second dash to varying degrees of prominence is not uncommon. Ventral color usually lighter shade than above, unremarkable without bands or maculation, length  $\bar{x}$  = 27.35 mm (25–31.5;  $n$  = 40). Hindwing: Unicolorous charcoal gray dorsally without whitish scales or maculation. Ventral surface as described for forewing. Genitalia: ( $n$  = 12) Valve generally oval, process of sacculus variable, narrow to broad projection, either acuminate, dentate, or combination of both, uncus apex mildly hooked (Fig. 2A).

**Female.** Head: As described for male. Antennae simple, length  $\bar{x}$  =

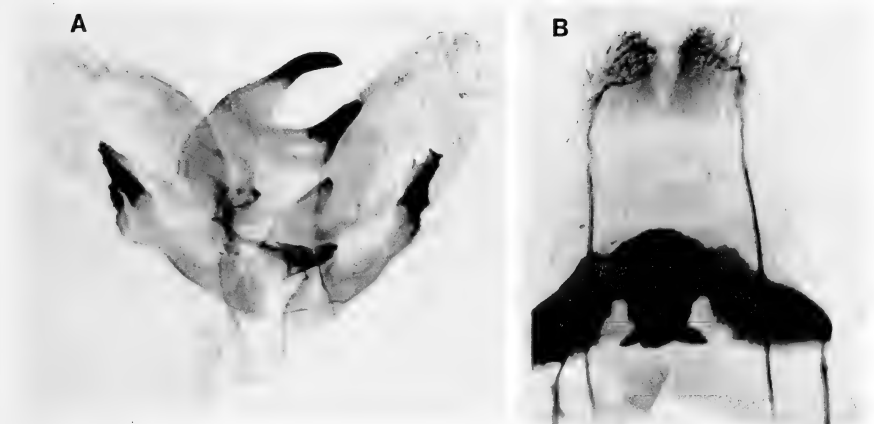


FIG. 2. Genitalia of *L. phaeobrachycerous*, Louisiana, St. Tammany Parish, A. male, B. female.

10.6 mm (10.0–12.0;  $n = 18$ ). Thorax: As described for male. Forewing: Dorsal and ventral color as described for male, length  $\bar{x} = 31.6$  mm (29.5–35.5;  $n = 14$ ). Hindwing: Dorsal and ventral color as described for male. Genitalia: ( $n = 4$ ) Sclerotized genital plate, rounded center convexity along distal edge. Entire structure unremarkable otherwise (Fig. 2B).

**Types.** Holotype ♂ (Fig. 1A), USA, Louisiana, St. Tammany Parish, 4.2 miles (6.8 km) NE Abita Springs, sec. 24T6SR12E, 9 Sept. 1991. Allotype ♀ (Fig. 1B), same locality, 19 Sept. 1991. Paratypes: 879 ♂ and 18 ♀, same locality, April 1 to Oct. 23, 1983–92. Holotype and allotype deposited in U.S. National Museum of Natural History. Paratypes deposited in Florida State Collection of Arthropods, Gainesville, Louisiana State University, Baton Rouge, and the author's collection.

**Diagnosis.** In contrast to *L. phaeobrachycerous*, scales on the front and vertex of the head of *L. coniferarum* form an acute distal projection between the antennae and lower margin of the frons, among Louisiana and Mississippi specimens.

Maculation is variable within populations, especially among different broods. In Louisiana, individuals of the first brood of *L. coniferarum* are larger than those of subsequent broods, a trait seen in other Louisiana Sphingidae such as *Isoparce cupressi* (Bdv.). The first brood of *L. coniferarum* also exhibits the greatest variation in color and shade. Specimens can be very dark, or have a predominance of brown scales especially on the forewings. It is not uncommon for darker specimens to exhibit a range of very dark gray to off-white or even near white hindwings.

In Louisiana, both *Lapara* species exhibit varying shades of gray or occasionally brownish gray. An area along the forewing inner margin between the transverse postmedial line and the base is chestnut brown in both species. In fresh specimens of *coniferarum*, the dorsal forewing ground color is usually ash gray. Unlike *phaeobrachycerous*, the entire dorsal surface of the forewing of *coniferarum* is suffused with white scales. In both species, these scales are especially concentrated basad of the along the postmedial line. The upper surface of the hindwing of *coniferarum* is noticeably lighter than the forewing, owing to white scales, which are more numerous near the base. This pattern occurs to a lesser degree in *phaeobrachycerous* but is absent in some specimens, the moths appearing unicolorous gray. Some *coniferarum*, usually individuals of the first brood, also have unicolorous gray hindwings.

Among the sparse forewing maculation of *Larara* are bold to faint black streaks occurring as a furcating transverse postmedial line, especially on the veins between the postmedial line and the outer margin. These black vein lines flare out as they approach and include the fringe near each vein. The fringe between each vein is usually white in *coniferarum* and white to off-white in *phaeobrachycerous*.

The forewing maculation of both species includes a faint to bold median line, which arises from the chestnut-colored area along the inner margin and proceeds towards the apex. The upper one-third of this line abruptly turns inwardly and intersects the costal margin at varying angles, acutely to near perpendicular. In *phaeobrachycerous*, this line often intersects the costal margin more basad than seen in *coniferarum*. The sometimes faint antemedial line roughly parallels the median line.

Riotte (1972) noted that female *L. coniferarum* have less accentuated markings than males. Markings of both Louisiana species similarly exhibit less accentuated markings. The forewing postcellular dashes vary in number in both Louisiana species. In *coniferarum* there are usually two dashes, though one or three occur in varying degrees of prominence and with less frequency. Visually, males of the two species are easy to distinguish. Male *phaeobrachycerous* appear as darker, slightly smaller, short and narrow-winged specimens with short antennae. The antennae of male *coniferarum* in Louisiana average 29% longer,  $\bar{x} = 13.3$  mm (11.5–14.5;  $n = 40$ ), than in *phaeobrachycerous*. Differences in both wing length and antennae length of *coniferarum* and *phaeobrachycerous* are statistically significant as defined by *t*-test (highest level  $\alpha = 0.0005$ ). In males of *coniferarum*, the antennae cilia are twice the length of those on *phaeobrachycerous*, while the shaft diameter is roughly equivalent in both species.

In Louisiana, the average forewing lengths for *coniferarum* are:



males  $\bar{x}$  = 29.25 mm (27.5–31.5;  $n$  = 40), females  $\bar{x}$  = 31.1 mm (29.5–35.0;  $n$  = 23). Riotte (1972) listed measurements for *coniferarum* as males 24–30 mm ( $n$  = 40), females 27–36 mm ( $n$  = 8), with no averages given. For *L. halicarnie*, Riotte listed forewing lengths as males 29–36 mm ( $n$  = 13), females 32–40 mm ( $n$  = 6).

The genitalia of *L. coniferarum* have been illustrated by Rothschild and Jordan (1903), Hodges (1971), and Riotte (1972). Both Riotte and Hodges discuss the variability of certain structures of the male genitalia, and Riotte illustrates the variation in the sacculus. Comparing female specimens from Louisiana, the distal edge of the lamella postvaginalis of *L. coniferarum* is gently rounded, without the degree of convex protrusion noted in *L. phaeobrachycerous*. This genital plate attribute does vary slightly over *L. coniferarum*'s vast range.

**Distribution.** Despite extensive collecting throughout Louisiana, *L. coniferarum* has been taken only in six upper, southeastern parishes, all east of the Mississippi River: West Feliciana, East Feliciana, East Baton Rouge, Ascension, Tangipahoa, and St. Tammany. This region of the state is known as the Florida Parishes.

I have studied hundreds of *Lapara* specimens from Mississippi to Florida, and upwards along the east coast states to Pennsylvania. From Georgia and South Carolina, specimens exist along with *coniferarum* which appear assignable to neither *coniferarum* nor *bombycoides*. They appear as small, narrow-winged specimens, like *phaeobrachycerous*, and may account for prior literature records indicating *bombycoides* occurring south to Florida. Due to limited material, it is unclear if these specimens have a relationship to *phaeobrachycerous*, though I suspect they are indeed *phaeobrachycerous*. All specimens examined from the area around Clemson, South Carolina, were melanic (very dark charcoal gray to near black) narrow-winged small specimens with short antennae.

The verified range of *L. phaeobrachycerous* includes only the states of Louisiana and Mississippi at present. Besides the type locality, specimens have been collected at Fluker, Tangipahoa Parish, Louisiana, and from Harrison, Pike, and Lee counties in Mississippi.

**Etymology.** The specific epithet is derived from the Greek *phaeo*, meaning dark, dusky, and *brachycerous*, meaning short horns or antennae.

## DISCUSSION

*Lapara* is a difficult genus for several reasons. Most field collected specimens are worn because the moths have a tendency to flutter along the ground through brush and leaf litter for considerable distances, especially when they approach light traps operating within a few feet of ground level. This problem appears to be reduced by operating traps

at a greater height above ground, for example, above five meters. Females comprised less than one percent of the total *Lapara* specimens collected. Apparently, females are not attracted to ultraviolet light to the degree males are.

In Louisiana, flight periods of *L. coniferarum* are different from those of *L. phaeobrachycerous*, though both species have five annual broods. Based on dates of capture over a seven-year period (1986–92), *L. coniferarum* has its initial annual brood peaking mid-April, with specimens beginning to appear in mid-March, and on occasion even as early as late February. The initial brood peak is separated from the second brood peak by an approximately two-month interval. Brood peaks two through four begin around mid-June and occur at 30-day intervals. In contrast, *L. phaeobrachycerous* has its first brood peak about mid-May, though the numbers of individuals of this brood are usually quite low compared to subsequent broods. All five broods occur at 30-day intervals.

Koebele (1881) stated that *L. coniferarum* has at least two annual broods in the southern United States. Riotte (1972) also stated *coniferarum* has two distinct flight periods in the southeastern coastal states. Those authors apparently did not recognize that their second brood/flight period involved multiple sequentially occurring broods.

Based on specimens collected at ultraviolet light traps, the nightly flight time for male *coniferarum* in Louisiana begins about midnight and lasts for approximately three to four hours, while females have appeared only at dusk. No flight time information is known about *phaeobrachycerous*.

Nothing is known about the immature stages of *phaeobrachycerous*, but I suspect that the larvae may feed on *Pinus* species. The area in which this new species occurs in Louisiana is classified as a longleaf pine region.

Specimens fade quite rapidly. Pinned specimens several years old appear brown, quite different in color than freshly collected specimens. This is due in part to ultraviolet degradation as well as the effects of chlorine gas from vaporizing insect pest fumigants in storage cases (Brou 1991). Descriptions of colors and other attributes are representative of those occurring on freshly collected and dried Louisiana specimens, unless stated otherwise. Clark (1919) commented that the type of *L. halicarnie* in Strecker's collection appears faded.

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## PROFILE

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### WILLIAM WITTFELD: THE FLORIDA CONNECTION

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**ABSTRACT.** William Wittfeld (1828-1913) collected numerous natural history specimens, including Lepidoptera, at "Indian River, Florida," in the vicinity of Georgiana, Brevard County. Many of his Lepidoptera specimens were sent to William H. Edwards, Henry Edwards, and Berthold Neumoegen. No fewer than thirty-three taxa of Lepidoptera were described from material collected by Wittfeld. He contributed to the life history descriptions of at least nineteen species. Three patronyms of Lepidoptera honor Wittfeld. His daughter, Annie M. Wittfeld (1865-1887), also reared numerous species.

**Additional key words:** Lepidoptera, "Indian River, Florida," type locality, life history, Annie M. Wittfeld.

During the late nineteenth century, Florida was still largely a vast, undeveloped frontier. New railroad systems were allowing pioneers to establish homesteads in formerly remote Indian territory. In 1880, the entire population of Florida totalled less than 270,000 (Tebeau 1980). In March of that year, William Wittfeld (1828-1913) began collecting Lepidoptera at his home on "Indian River, Florida." Wittfeld's specimens and observations of Florida species became invaluable to the prominent Lepidopterists of the period. For more than a decade, "Indian River, Florida" was a renowned source of unique and undescribed species of Lepidoptera.

William Wittfeld (Fig. 1) was born in Germany on 3 April 1828. In 1853, when he was 25 years old, Wittfeld immigrated to the United States, joining thousands of others seeking to escape political unrest in Germany. He left behind a large family, including sisters Hermine and Marie and brothers Herrmann, Hoeinreich, and Peter (Peter immigrated to the United States in 1869). William lived in Philadelphia where he worked as a bookkeeper. Here, he married Rosalie Gottlieb in 1863, with whom he had two children: Annie, born in 1865, and Harry, born in 1867. During Wittfeld's residency in Philadelphia, the city experienced "the coldest winter on record" (Weigley 1982). From that time forward, Wittfeld probably yearned for a milder climate.

Lured by the prospects of comfortable temperatures and available land, the Wittfelds moved in 1869 to Merritt Island, Florida where they

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FIG. 1. William and Rosalie Wittfeld at "Fairyland" (ca. 1890).

were among the first settlers (Hellier 1965). In May 1870, Wittfeld applied for a federal land patent to secure 376 hectares (152 acres) of fertile land on what is now the southern end of Merritt Island, just south of the town of Georgiana in Brevard County. The property rose in a long slope from the Indian River (an inshore marine habitat, now part of the Intracoastal Waterway), eastward across a narrow peninsula to the shores of the Banana River (a marine lagoon). Wittfeld could view both bodies of water from the top of this slope, which he called Honeymoon Hill. Into the side of the hill, Wittfeld dug a hurricane shelter nearly large enough to stand in. Forests of live oak (*Quercus virginiana* Mill.) and cabbage palm (*Sabal palmetto* (Walt.) Lodd ex Schultes) dominated the hill overlooking a clear lake that Wittfeld appropriately named Honeymoon Lake.

Wittfeld cultivated tropical fruits such as pineapples, bananas, and citrus. He also grew a variety of tropical plants that he generously distributed to his neighbors. His home was built next to a large Indian midden and burial mound and for many years was considered a "show-place" on the island (McAleenan 1991). Wittfeld started a school for his children next door to their home, bringing in a teacher who lived in a room adjoining the classroom. Over the years, Wittfeld developed his property into what he called "Fairyland" (or "Fairy Land"), which

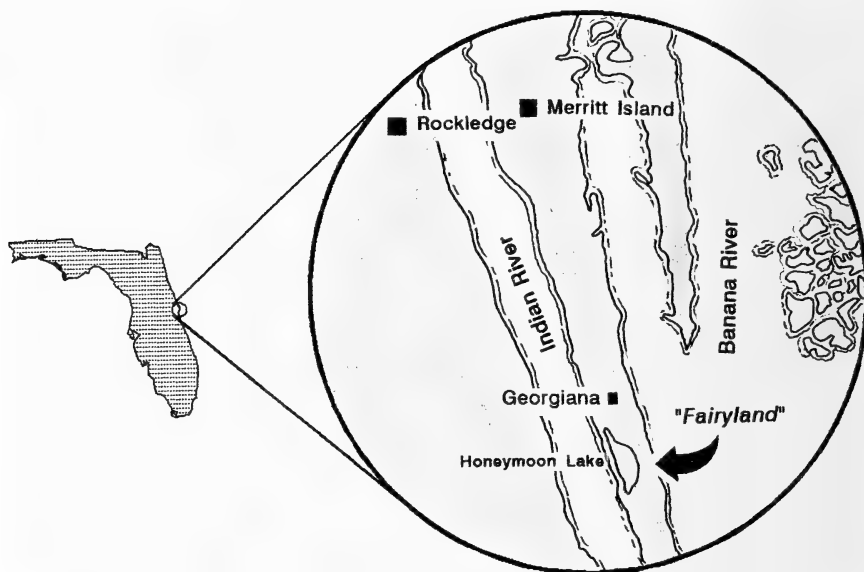


FIG. 2. Location of "Fairyland" in Brevard County, Florida.

became a popular tourist attraction during the late 1880's (Fig. 2). Tourists rented rooms within five cottages built adjacent to Wittfeld's home and strolled along trails that meandered through the local forest and around Honeymoon Lake. Although Wittfeld preserved much of the original landscape, developmental pressures began to have an effect on surrounding properties as early as the 1890's. Holland (1898) and Skinner (1907) both mentioned the destruction of a natural area near Wittfeld's home due to expanding cultivation.

At least seven different spellings of Wittfeld's name have been employed. William H. Edwards consistently misspelled his name as "Wissfeld" in letters to Henry Edwards during 1880 and 1881. This spelling was published at least three times (W. H. Edwards 1881a, 1881b, Neumoegeen 1881) and was the result of Wittfeld's own signature which closely resembled "Wissfeld." Additional spelling variations include Whitfeld (McAleenan 1991), Whitfeldt (Langlais 1984), Whittfeld (Anonymous 1913), Whitfield (Kjerulff 1972), Wittfield, and Whittfield (W. H. Edwards 1882d, H. Edwards 1883b, U.S. Census Bureau 1900, Hellier 1965). Although he was usually referred to as "Dr. Wittfeld" and W. H. Edwards (1881f) stated that Wittfeld was a "physician," it is unclear whether he ever practiced medicine or the title was granted out of respect for his horticultural expertise (e.g., "herb doctor"). Wittfeld was congenial, educated, spoke eloquent English, and had a predilection for smoking cigars.

Wittfeld's botanical interests eventually led to a fascination with insects, especially Lepidoptera. In March 1880, Wittfeld contacted W. H. Edwards about his desire to collect insects. Edwards persuaded his sister and her husband, who resided at Lake Jessop, Florida, to visit the Wittfelds during a trip to the Indian River region. She convinced Wittfeld to collect Lepidoptera specimens for Edwards who generously forwarded the necessary equipment including nets, poison, and insect pins. It appears that Wittfeld also agreed to collect a limited number of Coleoptera specimens at the request of W. H. Edwards, but the disposition of these specimens is unknown.

Shipments of specimens from Wittfeld were eagerly accepted by Edwards who retained only the butterflies, offering the moths (and duplicate butterflies) to Henry Edwards and Berthold Neumoegen. As an incentive to Wittfeld, W. H. Edwards suggested that H. Edwards and Neumoegen begin contributing money to Wittfeld for the specimens they received ("it will be well and encouraging"). To facilitate this endeavor, W. H. Edwards proposed a fixed price of 10 cents each for the desirable specimens. Edwards collected these payments and forwarded them directly to Wittfeld. Over the next twelve years, Wittfeld and W. H. Edwards developed a close relationship.

During 1880 and 1881, Wittfeld supplied thousands of specimens to W. H. Edwards, H. Edwards, and Neumoegen. Individual shipments consisted of 500 or more specimens. In a letter dated 10 December 1880, W. H. Edwards proposed to H. Edwards that Wittfeld could supply them four thousand specimens during 1881 for a fee of two hundred dollars. W. H. Edwards continued to instruct Wittfeld in proper collecting techniques and sent additional equipment especially suitable for collecting moths.

As with many nineteenth century naturalists, Wittfeld's passion to collect was not limited to one group of organisms. In February 1881, Wittfeld contacted Spencer F. Baird of the Smithsonian Institution and offered to collect snake specimens for the National Museum. He explained that collecting Lepidoptera and Coleoptera "does not occupy all my time." Wittfeld ultimately supplied Baird with numbers of small mammals, snakes, turtles, frogs, lizards, fish, shells, and a few insects (Coleoptera and Orthoptera; to be forwarded to W. H. Edwards if unwanted). All these specimens were shipped in jars of alcohol which Baird supplied. Wittfeld also procured some Indian artifacts for the museum. Baird paid Wittfeld for this material and based compensation on rarity.

It is apparent that Wittfeld's inexhaustible collecting activities occasionally exceeded the demand for his specimens, especially of "common" species. In late 1881, Henry Edwards complained about having

to pay Wittfeld for all the specimens he had received. In response, W. H. Edwards wrote Wittfeld and asked him to reduce the number of shipments and to "collect only the rarest in such as he conveniently can and not give all his time to it as he has been doing." S. F. Baird also advised Wittfeld (letter dated 27 March 1882) that many of the specimens he was sending were of little value to the Smithsonian collections. Despite the consistency of Wittfeld's shipments, payments were sometimes painfully tardy. Delinquent payments were further exacerbated by uncontrollable postal delays. W. H. Edwards lamented that Wittfeld's letters were "sometimes 10 or 11 days in getting to me . . . and mine to him just the same." Hardships associated with life in Florida also contributed to delays in shipments and payments.

In 1881, Wittfeld bemoaned the hordes of mosquitoes he encountered whenever he attempted to collect, resulting in a reduction in the number of specimens he was able to secure. It is notable that one of the highest densities of mosquitoes ever recorded in Florida was near Wittfeld's home in Brevard County where early residents of Merritt Island supposedly escaped mosquito bites by stuffing their clothing with crumpled newspaper (Myers and Ewel 1990). In September 1880, the Wittfelds were nearly devastated by a hurricane. W. H. Edwards was greatly concerned about their welfare and wrote (letter to H. Edwards dated 11 September 1880) that he feared that Wittfeld "suffered by the late cyclone on that coast. Since that occurred I have had no letter from him. He has not missed a mail for months." Edwards' fears were partially realized when Wittfeld confirmed that the hurricane "nearly ruined them." The damage was severe. The storm "blew all the leaves off trees, tore down fences and buildings (but not his house), broke off all ripe oranges, broke flat the bananas" and "pulled pine apples from the roots." As a result of the hurricane, Wittfeld temporarily suspended shipments of specimens to Edwards. The storm had damaged the mail boat, causing the mail to run so irregularly that he could not trust boxes to it. Surprisingly, Wittfeld resumed shipments to Edwards by early October of that year.

Wittfeld soon became concerned that the increasing popularity of his captures would result in unwanted requests for specimens. In April 1880, he asked W. H. Edwards to keep his name as confidential as possible. Only W. H. Edwards, H. Edwards, Neumoegen, and E. T. Cresson, Sr. were initially aware of Wittfeld's identity. In January 1881, W. H. Edwards reminded H. Edwards not to publish Wittfeld's name "for fear that it will lead to everybody writing him for butterflies." Four months later, W. H. Edwards inexplicably ignored his own advice and published Wittfeld's name (as "Wissfeld") (W. H. Edwards 1881a).

In early 1882, Wittfeld sought to provide specimens of *Papilio* to the



German entomologist, Otto Staudinger, while reserving the right to continue supplying material to W. H. Edwards and Neumoegen. After 1883, shipments from Wittfeld became increasingly irregular. Very few shipments were sent during the late 1880's. The correspondence between Wittfeld and W. H. Edwards appears to have ceased in 1892. The Smithsonian Institution continued to receive small mammals and reptiles from Wittfeld until at least 1894.

No fewer than 33 taxa of Lepidoptera were described from Wittfeld material and possess type localities of "Indian River, Florida." They are currently included in the families Tineidae (Beutenmueller 1887), Yponomeutidae (H. Edwards 1881a), Sessiidae (H. Edwards 1883b), Hesperidae (W. H. Edwards 1880a, 1881e, Lintner 1881, Skinner 1896), Pieridae (Skinner 1894, Miller and Brown 1981), Lycaenidae (W. H. Edwards 1883), Nymphalidae (W. H. Edwards 1880b), Limacodidae (H. Edwards 1886), Pyralidae (Hulst 1886, Kimball 1965), Geometridae (Grote 1882, Kimball 1965), Arctiidae (H. Edwards 1882, 1883a, Neumoegen 1881), Apatelodidae (H. Edwards 1886), Sphingidae (Butler 1881), and Noctuidae (Grote 1884, H. Edwards 1881b, 1886, Kimball 1965). Wittfeld also discovered a new species of muskrat (Rodentia: Cricetidae) (True 1884).

Wittfeld was the first to confirm the occurrence of several species of Lepidoptera in North America, including *Battus polydamas* (L.) (W. H. Edwards 1882a, 1882d), *Hypolimnys misippus* (L.) (W. H. Edwards 1881d, 1888b), and *Siproeta stelenes* (L.) (W. H. Edwards 1885). Edwards was constantly impressed by the species that Wittfeld found, telling H. Edwards (letter dated 17 July 1881) "one Cuban or Mexican species after another turns up there." In addition to supplying dried adult specimens, Wittfeld also reared many species and sent W. H. Edwards live and preserved examples of ova, larvae, and pupae. Many of the preserved early stages of moths were forwarded to H. Edwards.

W. H. Edwards personally reared many species of Lepidoptera from ova and larvae supplied by Wittfeld. Edwards had a particular fondness for *Heliconius charitonius* (L.). With the assistance of Wittfeld, Edwards reared this species numerous times and published a description of its early stages (W. H. Edwards 1881c). On 27 May 1880, Edwards wrote "I turned a ♂ *Heliconia Charitonias* loose (from chrysalis) in my parlor yesterday and it was pretty to see it course about just as I remember adult *Heliconias* on the Amazon." The behaviors of adult *H. charitonius* were carefully documented by Wittfeld and published by W. H. Edwards (1881f). Wittfeld's specimens and detailed observations contributed to the life history descriptions of at least nineteen species of Lepidoptera (see W. H. Edwards 1881a, 1881b, 1882b, 1882c, 1887-97, H. Edwards 1887, Scudder 1889). W. H. Edwards (1883)

wrote that Wittfeld "has done more to elucidate the biological history of the Lepidoptera of Florida than any one who has preceded him."

Additional references to Wittfeld, "Indian River" or Georgiana, Florida can be gleaned from over one hundred years of literature on Lepidoptera. Such sources include W. H. Edwards (1881g, 1884b), French (1885), Maynard (1891), Skinner (1911, 1921), Grossbeck (1917), Skinner and Williams (1924, 1925), Burns (1964) and Kimball (1965). Holland (1898, 1903, 1931) photographed several of Wittfeld's specimens for his plates. Wittfeld's specimens are also discussed in detail by Brown (1967, 1970), Brown and Miller (1975, 1977, 1980, 1987), and Calhoun (1993). Most major North American institutional collections possess Wittfeld Lepidoptera specimens.

Annie M. Wittfeld shared her father's interest in Lepidoptera. In September 1884, Annie documented the strange effects that a lightning strike had on the larvae of *Limenitis archippus floridensis* Strecker (W. H. Edwards 1884a). She was a talented artist and occasionally supplied drawings of new captures and early stages of Lepidoptera to W. H. Edwards. Some of the life history information attributed to William Wittfeld is actually referable to Annie. In November 1887, Annie observed *H. misippus* ovipositing on purslane (*Portulaca* sp.) and subsequently reared the species on this plant (W. H. Edwards 1888b, dos Passos 1951). This remains one of only two known records of *H. misippus* reproducing in North America. W. H. Edwards (1888b) characterized Annie as "intelligent and painstaking." Unfortunately, on 10 April 1887, Annie died of rheumatic fever at the age of 23 (W. H. Edwards 1888a). Fifteen months earlier, on 10 January 1887, the Wittfelds' only son, Harry, died suddenly of meningitis at the age of 20 after becoming ill on a boat trip down the Indian River. William and Rosalie were devastated by these losses. It is likely that these tragedies contributed to William's decreasing contact with W. H. Edwards and the Smithsonian Institution during the late 1880's.

The final blow to William occurred with the death of his wife on 16 December 1906. She was interred with Annie and Harry under a large oak tree near their home at "Fairyland." In 1911, their remains were relocated to the Georgiana Cemetery. William's health gradually failed. During the closing years of his life, he was cared for at the home of his friends, Mr. and Mrs. John Frye, of Rockledge, Florida. It was here that William Wittfeld died of edema on 13 July 1913 at the age of 86. We was interred beside his wife and two children at Georgiana Cemetery.

Today, there is little evidence of "Fairyland" or the habitats that Wittfeld frequented. Honeymoon Lake is nearly surrounded by housing

developments. Nevertheless, neighboring properties still support tropical plants that grew from Wittfeld's cuttings.

### Patronyms in Lepidoptera named in honor of William Wittfeldt:

*wittfeldtii*, W. H. Edwards, *Thecla*, 1883, Canadian Entomol. 15:136-137.

*wittfeldii*, H. Edwards, *Alypia*, 1883, Papilio 3:34.

*wittfeldii*, H. Edwards, *Pyrohotaenia*, 1883, Papilio 3:156.

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## GENERAL NOTES

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### MUSINEON TENUIFOLIUM (APIACEAE): NEW HOST OF FOUR NEBRASKA PAPILIO (PAPILIONIDAE)

**Additional key words:** *Artemisia dracunculus*, *Papilio machaon*-complex, swallowtail.

The recorded larval host plants of four *Papilio* species, *P. zelicaon nitra* W. H. Edwards, *P. indra* Reakirt, *P. polyxenes asterius* Fabricius, and *P. machaon bairdii* (W. H. Edwards), encompass a variety of genera in three plant families, Asteraceae, Apiaceae, and Rutaceae. Here we report narrow-leaved musineon, *Musineon tenuifolium* Nutt. (Apiaceae), as a new larval host plant for these four swallowtails.

*Musineon tenuifolium* is endemic to the west-central Great Plains, ranging from the Black Hills of South Dakota and Wyoming, south through eastern Wyoming and the Nebraska panhandle (Barkley 1977). Farrar (1990) characterizes *M. tenuifolium* as a native perennial favoring dry, rocky outcrops, growing from a caudex atop a thickened taproot. It possesses stemless, dissected leaves rising from a root crown to form a compact tuft of foliage. Small, cream to bright yellow flowers form compound umbels, approximately 2.5 cm across, atop a leafless stalk normally less than 15 cm tall. In Nebraska, *M. tenuifolium* usually stays green the entire season except under severe drought conditions. It is an extremely local umbel, but often common in the appropriate habitat.

*M. tenuifolium* was first brought to our attention in 1983 while collecting in the canyons of northwestern Sioux County, Nebraska. A search of *M. tenuifolium* foliage yielded larvae of both *P. z. nitra* and *P. indra*. *M. tenuifolium* is believed to be the exclusive host plant for these swallowtails in Nebraska, and supports a second brood of *P. indra* in our area. We also have observed larvae of *P. z. nitra* and *P. indra* feeding on *M. tenuifolium* in the Black Hills of South Dakota.

On 20 June 1991, a collecting trip to Bull Canyon, Banner County, Nebraska resulted in about 40 swallowtail larvae collected on *M. tenuifolium*. Of these larvae, approximately one-half emerged as adults from mid-July through mid-August. Surprisingly, only three adults were *P. z. nitra*; others were *P. p. asterius*.

While collecting in southern Scotts Bluff County, Nebraska on 25 May 1992, five 5th instar swallowtails were discovered on *M. tenuifolium* by the first author and Nick D. Theis. The larvae were removed and fed cut *M. tenuifolium* until pupation. Starting 15 June 1992, pupae began to eclose. Emergent adults were *P. m. bairdii*, a species thought to have fed exclusively on silky wormwood, *Artemisia dracunculus* L. (Asteraceae), in Nebraska.

These observations raise some intriguing questions regarding possible range extensions and the use of alternative host plants by members of the *P. machaon*-complex. It is likely that continued efforts of naturalists and collectors within and outside the state will lead to insights concerning these and subsequent questions.

We thank Brett C. Ratcliffe and J. Ackland Jones for review of the manuscript. We are grateful to Neil E. Dankert and Jeff C. Germer, who assisted in collecting larvae. This is paper number 10264 of the journal series of the Nebraska Agricultural Research Division, University of Nebraska. This work was supported by the University of Nebraska Agricultural Experiment Station Project 17-055.

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## TWO NEW SYNONYMIES IN NEARCTIC *EUCOSMA* (TORTRICIDAE: OLETHREUTINAE)

**Additional key words:** *Eucosma wandana*, *E. uta*, *E. ustulatana*, Kentucky, genitalia.

In the course of identifying *Eucosma* specimens captured recently in Kentucky, we reached the conclusion that *E. wandana* Kearfott, *E. uta* Clarke, and *E. ustulatana* Blanchard & Knudson are one and the same morphospecies. Males captured at the same Kentucky locality on the same date match male holotypes of all three taxa. All specimens we examined that had been or could be assigned to these taxa have similar underlying forewing patterns varying in the proportion of dark brown to light orange brown. On average, males ( $n = 12$ ) are darker brown than females ( $n = 44$ ).

*Eucosma wandana* was described from one male by W. D. Kearfott in 1907, but we also have seen a female with a "type" label not mentioned in the original description; *E. uta* was described from two males and one female by J. F. G. Clarke in 1953; and *E. ustulatana* was described from two males by A. Blanchard and E. C. Knudson in 1983. None of these short type series reveals the full range of color variation we observed in longer series. Moreover, Clarke seems to have overlooked *E. wandana* when he described *E. uta*; for differentiation, he used *E. atomosana* (Walsingham), a western species (Heinrich 1923). In describing *E. ustulatana*, Blanchard and Knudson used *E. wandana* (as *E. eumaea* Meyrick) for comparison, but the diagnostic differences cited by them—smoother, more evenly convex anterior valvar margin in *E. ustulatana*—can be ascribed to individual variation. No differences are discernible among holotype genitalia of *E. wandana* (as *E. eumaea*) (Heinrich 1923), *E. uta* (Clarke 1953), or *E. ustulatana* (Blanchard & Knudson 1983).

We summarize as follows:

### *Eucosma wandana* Kearfott (Figs. 1–3)

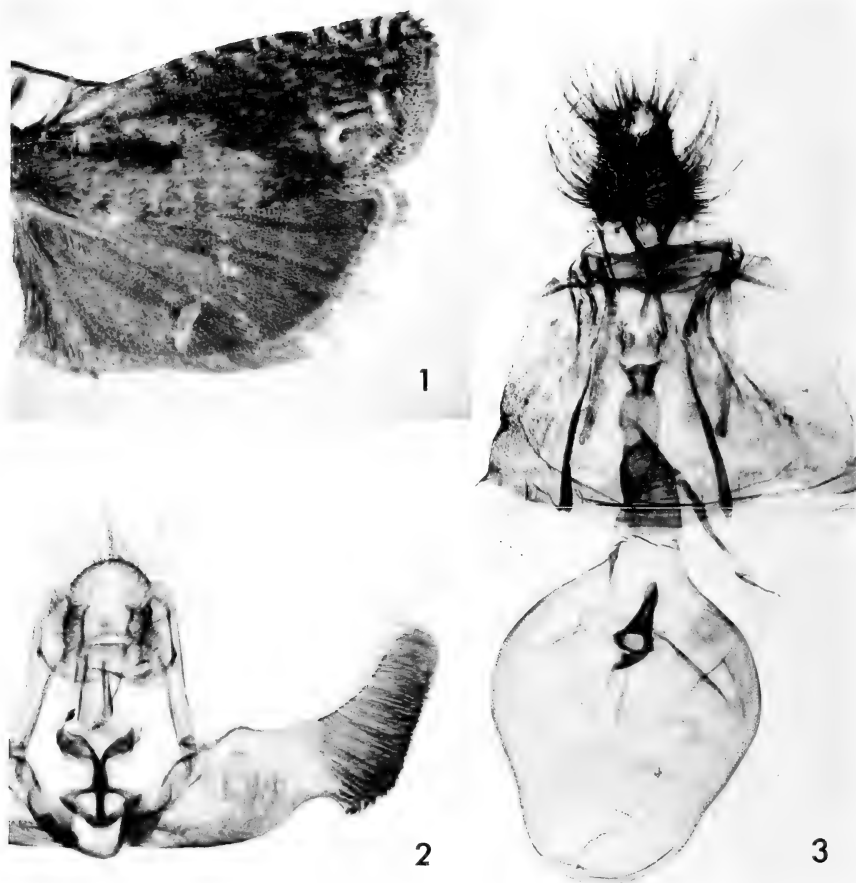
*Eucosma wandana* Kearfott (1907) (holotype: male, Cincinnati, Ohio, 25 July [not August as in original description] 1904, A. F. Braun, in American Museum of Natural History [AMNH], New York, N.Y., wings illustrated in Fig. 1 here); Klots (1942).

*E. eumaea* E. Meyrick (1912); Heinrich (1923) (holotype genitalia photo-illustrated); Klots (1942) (invalid replacement name).

*E. uta* Clarke (1953) (holotype: male, Putnam Co., Illinois, 10 July 1939, M. O. Glenn, in National Museum of Natural History [NMNH], Washington, D.C.; male and female genitalia sketch-illustrated, wings of paratype photo-illustrated); Godfrey, et al. (1987) wing of female photo-illustrated. **New Synonymy.**

*E. ustulatana* Blanchard & Knudson (1983) (holotype: male, Brenham, Washington Co., Texas, 4 June 1979, E. C. Knudson, genitalia prep. WEM 36924, in NMNH, wings photo-illustrated, male genitalia of paratype photo-illustrated). **New Synonymy.**

*Eucosma wandana* is probably multivoltine. Capture dates range from 4 June to 15 September ( $n = 53$ ). The known distribution is Kentucky, Ohio, Illinois, Missouri, Arkansas, Kansas, Georgia, Florida, and Texas. Forewing length of males ranges from 7.5 to 8.5 mm ( $n = 12$ ); of females, 7.0 to 9.25 mm ( $n = 44$ ). *Eucosma wandana* is one of at least 11 eastern species of *Eucosma* having ventral extensions of female papillae anales (Fig.



FIGS. 1-3. *Eucosma wandana*. 1, Wings of holotype. 2, Genitalia of male. 3, Genitalia of female.

3), an accessory whose function is not yet known (Miller 1987). The larval food plant is unknown.

We thank F. H. Rindge, G. L. Godfrey, K. R. Methven, J. R. Heitzman, and D. Profant for specimen loans.

**Material examined.** We examined specimens as follows, labeling all except primary types "Voucher, Gibson & Miller 1992": ARKANSAS: Devil's Den St. Pk., Washington Co., one male, 6.VII.66; one female, 6.VII.66 (genit. prep. USNM 70317); one female, 26.VI.66; one female, 3.VII.66 (genit. prep. USNM 70316) all R. W. Hodges; Washington Co., "type", female. KANSAS: Pittsburg, E. L. Todd, one female, 28.VI.54; one female, 2.VII.54. GEORGIA: Atlanta, P. W. Fattig, one male, 31.VII.41. TEXAS: *E. ustulatana* holotype; Dallas, "714", Fernald collection, one female (all foregoing in NMNH). OHIO: *E. wandana* holotype (in AMNH). KENTUCKY: Campbell Co., Jolly Co. Pk., three females, 15.VII.82 (female genit. prep. LDG 134) (Fig. 3); Gallatin Co., Markland Dam, two females, two males, 3.VIII.88 (male genit. prep. LDG 048) (Fig. 2); Boone Co., Big Bone Lick St. Pk., one female, 7.VII.81; one female, 27.VII.89; Owsley Co., near Boone-



ville, two females, two males, 22.VI.84 (male genit. prep. LDG 047); Bullitt Co., near Shepherdsville, one female, 8.VII.88 (all L. D. Gibson, in L. D. Gibson collection). MISSOURI: Cape Girardeau, one female, 25.VII.78; Independence, one male, 30.VI.76; Clay Co., Coolie Lk., one female, 18.VII.68; one female, 22.VII.72 (all J. R. Heitzman, in J. R. Heitzman collection). ILLINOIS: *E. uta* holotype; Oconee, two females, 8–15.VII; one female 1–7.VII (female genit. prep. USNM 70670); Decatur, one female, 8–15.VII; Putnam Co., M. O. Glenn, one female, 30.VII.74; one male, 18.VII.73; one female, 3.VIII.65; one male, 25.VII.74 (male genit. prep. WEM 176923); one female, 13.VIII.43 (female genit. prep. USNM 70320) (*E. uta* paratype); (all in NMNH); Putnam Co., M. O. Glenn, one male, 23.VI.56, "5057"; one male, date missing, "5157"; one female, 5.VII.53; one female, 24.VII.68; one female, 11.VIII.74; one female, 15.VII.64; one female, 5.VIII.61 (abdomen missing); one female, 28.VII.64; one female, 2.VII.56; one female, 15.IX.54; one female, 28.VII.56; one female, 21.VII.56; one female, 23.VII.73; one female, 10.VII.39; one female, [illegible].VII.65; one female, 17.VII.64; one female, 29.VI.64; one female, 5.VIII.47 (*E. uta* paratype) (all in Illinois Natural History Survey Collection). FLORIDA: Liberty Co., Torreya St. Pk., one female, 7.VII.88 (female genit. prep. LDG 131) (D. Profant, in D. Profant collection).

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ADDITIONAL DATA ON THE GEOGRAPHICAL DISTRIBUTION AND  
ADULT ACTIVITY OF THE DIURNAL, MIMETIC PLUME MOTH,  
*OIDAEMATOPHORUS CHAMELAI* (PTEROPHORIDAE)

**Additional key words:** Costa Rica, Mexico, *Croton*, *Cordia*.

An extraordinary, black pterophorid with enlarged scale tufts on the hind legs was described from Mexico by Gelis (1992), but neither its strikingly wasp-like appearance

nor its diurnal behavior, unusual for the family, were emphasized. In addition to the type series of seven specimens, most of which were collected by Chemsak in 1985–86, we have taken a larger number in more recent years, documenting a more extensive flight period. Moreover, two specimens from Costa Rica were erroneously recorded from Mexico by Gielis.

**Geographical distribution.** *Oidaematophorus chamelai* has been recorded along the immediate Pacific coast of Middle America, in Mexico near Elota in central Sinaloa, and Chamela, Jalisco, and in northwestern Costa Rica in Guanacaste Province. An inland occurrence in Mexico, indicated on the mapped distribution by Gielis in the vicinity of Guadalajara, evidently was based on his misinterpretation of the label on specimens from Costa Rica ("C.R.: Playa Tamarindo, Guan. Prov.") as the State of Guanajuato, Mexico. A specimen from south of Elota, Sinaloa, was illustrated and cited but not mapped.

**Seasonal occurrence.** In Mexico we have taken adults of *O. chamelai* during each month that we have visited the Estación de Biología Chamela: July, August, September, October, December; while the Costa Rica specimens were collected in June. Whether or not the species flies during the dry season (December–June in Mexico, January–April in Costa Rica) cannot be determined from our sampling.

**Mimetic appearance and diurnal activity.** *Oidaematophorus chamelai* and two closely related South American species, *O. ochracealis* (Walker) and *O. paraochracealis* Gielis, differ markedly from typical members of the genus in having the wings relatively broad and uniformly black with purplish iridescence or "brown-black" (Gielis 1992). *Oidaematophorus chamelai* is particularly wasp-like, an image enhanced by broad, cream-colored, dorsolateral spots on abdominal segments 2 + 3 that render the appearance of the constricted petiole of many ichneumonids and sphecids, and by seemingly aposematic red tegulae and large yellowish "eyespot" of the metathorax. Another pair of cream colored dorsal spots at the base of segment 8, which were lacking on the Sinaloa female Gielis illustrated, are variable from a trace to conspicuous in both sexes. The male has long, white, eversible hair brushes flanking the genitalia that were not mentioned by Gielis. The enlarged scale tufts of the hind tibiae (misinterpreted as the first tarsal segment in the original description) and tarsi in the male and tarsi only in the female are reminiscent of many ctenuchine Arctiidae, such as *Macrocne*, that are believed to be members of mimetic assemblages. D. L. Janzen has reared one species of *Macrocne* and two of the closely related *Poliopastea* from *Mesechites trifida* (Apocynaceae), a plant family well known for its cardiac glycosides. The diurnal, aposematic larvae and adults of these two genera are superficially quite similar and presumably are distasteful to vertebrate predators (Janzen in litt., Dietz 1994).

While nearly all Nearctic and Neotropical pterophorids that we have encountered are nocturnal, *O. chamelai* (and presumably the other species of the *O. ochracealis* complex) are primarily diurnal. We have observed adults of *O. chamelai* at flowers of three shrub and tree species of *Croton* (Euphorbiaceae) at the Estación de Biología Chamela. Their time of activity corresponded with that of other flower visitors such as cerambycid and scarabaeid beetles, wasps, bees, and hesperiids. In Costa Rica, males were collected by sweeping inflorescences of an arboreal *Cordia* (Boraginaceae), 5–6 m above the ground, employing an extensible tropical net. In addition, however, about 7 individuals of 17 taken at Chamela were attracted nocturnally to ultraviolet or white lights.

**Location of specimens.** The holotype is housed in the Essig Museum of Entomology, University of California, Berkeley (UCB), along with later collections. Specimens also are deposited in the Instituto de Biodiversidad, Santa Domingo de Heredia, Costa Rica (INBio); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (UNAM); Los Angeles County Museum of Natural History (LACM); U. California, Riverside (UCR); and the U. S. National Museum of Natural History, Washington, D.C. (NMNH). The type series was erroneously cited as LACM; the specimens had been on loan to J. P. Donahue from UCB and UCR and were so labelled when forwarded to Gielis, but their ownership was not communicated.

**Material examined.** COSTA RICA: Playa Tamarindo, Guan. Prov., 2 ♂, VI-14-86, "arboreal Croton fls. 15–18 ft. above ground, tropical net" (Chemsak, H. Katsura, A. & M. Michelbacher). MEXICO: Estacion de Biología Chamela, Jalisco, ♂ Holotype, ♀ VII-

8/16-85 (Chemsak, Katsura, Michelbacher); 2 ♂, ♀ X-13/23-86 (Chemsak); ♀ VII-12/15-87 (Chemsak & E. G. Linsley); 2 ♀ X-16/19-87, ♂ X-21/22-87, blacklight (Chemsak & Powell); ♂ IX-27/28-88, blacklight (P. A. Opler); ♀ XII-1-88 (Chemsak); 2 ♂, ♀ VII-23-90, 1 ♂ at light (Chemsak); ♀ VII-13-92, ♂ VII-20-92, at lights (Chemsak); 1 ♂, VII-15-93, at *Croton* flowers (B. Eya).

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## BOOK REVIEWS

KEYS TO THE INSECTS OF THE EUROPEAN PART OF THE USSR (G. S. Medvedev, chief editor). VOLUME IV (LEPIDOPTERA), PART II, by M. I. Falkovitsh (ed.) et al. 1990. E. J. Brill, Leiden. (translation of: OPREDELITEL NASEKOMYKH EVROPEISKOI CHASTI SSSR, TOM IV, CHESHUEKRYLYE, VTORAIA CHAST. Nauka Publishers, Leningrad, 1981—*translator*: B. R. Sharma). x + 1092 pp., 675 figs. Hard cover, 16 × 24 cm, ISBN 90-04-08926-8. \$160.00 U.S. Available from E. J. Brill (U.S.A.) Inc., 24 Hudson Street, Kinderhook, New York 12106.

This remarkable, bulky handbook is the second part of a work devoted to the Lepidoptera of western Russia. The English version of Part One was issued in 1987 (Amerind Publishing Co. Pvt. Ltd, New Delhi—edition supervised by the U.S.D.A., Washington, D.C.), and it covered the non-ditrysian families (with only a superficial treatment of the Nepticulidae), and eight families among the lower Ditrysia, namely the Psychidae and all members of the Zygaenoidea, Cossioidea, Sesioidea and Tortricioidea. Part Two deals with a larger number of families (29 if one accepts the classification that I proposed in 1991: see *Entomol. Scand.* 22:90-91). These are the Eriocottidae and Tineidae (including the "Euplocamidae" and "Hieroxestidae"), all members of the Gracillarioidea, Yponomeutoidea, Choreutoidea, Urodoidea (*Wockia* Heinemann: p. 508, as a "plutellid" genus), Schreckensteinioidae, and Epermenioidea, and all the gelechioid families with the exception of most Coleophoridae (only the Amphisbatinae being treated: pp. 792 and 801, among the Oecophoridae *sensu auct.*). Parts One and Two thus provide keys to the "Micromoths" of nearly all the families known to occur in the European part of Russia.

The present book is firmly bound in boards, nicely presented, and has a good quality paper, i.e., opaque and whiter than that of the Russian edition. Compared with the latter, the book is thicker (approximately 7 cm) and of a different format: 15.5 by 24 cm instead of 17.5 by 27 cm. Most figures, however, have not been reduced and are as good as those of the original publication. Only a few figures are less satisfactorily printed, such as Figures 191 and 193. The page numbers of the Russian original are mentioned in the lefthand margin, and thus often precede the numbers of the figures (which may be a bit confusing). The arrangement of the figures is usually rather practical, although it should have been slightly different in a few cases: for example, Figures 11 and 12 (*Euplocamus* Latreille) are found on page 16, in the "Key to suborders and families," whereas they correspond to the "Euplocamidae" text (pp. 24-25); Figures 499 to 505 (*Schreckensteinia* Hübner and *Heliodines* Stainton) should have been placed between the Schreckensteiniidae (pp. 697-698) and Heliodinidae (pp. 699-700), rather than at the end of the Stathmopodidae chapter; etc.

On the whole, the English translation appears quite faithful, and no changes were introduced, either nomenclatural or taxonomic. That is definitely a reasonable option, although typographical errors might have been rectified for certain Latin names. For instance, *Bucculatrix gnaphaliellae* (p. 193), *B. frangulella* (p. 195), *Caloptilia populatorum* (p. 252), *Milliereia* (p. 414), *Mompha propinguella* (p. 704), *Pseudatemella* (p. 792), and *Oliaria* (p. 1001), are all incorrect spellings for, respectively, *Bucculatrix gnaphaliella* (Treitschke), *B. frangutella* (Goeze), *Caloptilia populetorum* (Zeller), *Millieria* Ragonot, *Mompha propinquella* (Stainton), *Pseudatemella* Rebel, and *Uliaria* Dumont.

Nine authors contributed to Part Two, namely: A. S. Danilevsky (Choreutidae), M. I. Falkovitsh (Heliodinidae, Scythridae, Stathmopodidae, Schreckensteiniidae, Epermenioidea), Z. S. Gershenson (Yponomeutidae), V. I. Kuznetzov (Gracillariidae, Glyptopterigidae, Choreutidae), A. L. Lvovsky (Oecophoridae *sensu auct.*), V. I. Piskunov (Symmocidae, Lecithoceridae, Blastobasidae, Gelechiidae), S. V. Seksajeva (Bucculatricidae, Gracillariidae, Phyllocnistinae, Lyonetiidae), S. Yu. Sinev (Elachistidae, Batrachedridae, Momphidae, Cosmopterigidae), and A. K. Zagulajev (Tineoidea, Douglasiidae, Roeslerstammiidae, Urodidae, and several yponomeutoid and gelechioid families). Most of these entomologists are well known specialists of the families in question, so that the proposed keys are usually quite reliable. Sometimes they could not examine a number of foreign (European) species, their work in such cases being largely based on that of other specialists

(e.g., R. Gaedike's papers on Douglassiidae and Epermeniidae). Much in the same way, the drawings were made by several artists or even, sometimes, by certain of the above-mentioned lepidopterists. These illustrations range from fair to excellent, and are often original, though explicitly taken from other works in several cases. I would like to emphasize the abundance of the figures provided throughout the book: nearly 530 drawings represent adults or their wing pattern; nearly 240, wing venation schemata; about 1700 and nearly 470, male and female genital structures, respectively; and so on. As in Part One, photography was not used, probably because diagnostic features may be more easily distinguishable with line drawings.

After a short abstract (p. v), a preface (pp. vii-viii) and a table of contents (pp. ix-x), the handbook starts with a key to suborders and families (pp. 1-23). Elaborated by M. I. Falkovitsh and A. K. Zagulajev, this key is almost identical with that published in Part One, except for minor changes: the translation is better, abbreviations have been avoided, and illustrations are slightly more numerous. Various parts of the key are interesting and original, but a few remarks have to be made:

- \* many of the characters selected for a given family cannot be generalized on a worldwide scale
- \* according to the seventh alternative, tibial spurs would be absent from the Hepialidae, but they are actually present in genus *Gazoryctra* Hübner, one species of which is treated in Part One (as a member of *Korscheltellus* Börner)
- \* alternatives 13 and 22 are chiefly based on a slight difference in the "breadth" of the head, not on a clear-cut demarcation between two traits
- \* several inaccuracies must be corrected: ocelli are present in many Eriocottidae (contrary to alternative 16 statement), the maxillary palpi may be well developed in Adelidae since *Nematopogon* Zeller definitely belongs to this family (90), the Sesiidae possess a long frenulum (118), tympana are distinctly present in the Thaumetopoeinae (Notodontidae) (182), etc.
- \* "Endromidae" has been omitted after "In forewings R with 4 branches (R2-R5) stalked together" (alternative 190); in the description of the Nolidae (alternative 202), "ocelli" obviously represents a slip, and should be replaced by "compound eyes"
- \* the nomenclature is wrong or outmoded for certain groups: in particular, Brachodidae must be substituted for "Atychiidae," Saturniidae for "Attacidae," and Thyatirinae (Drepanidae) for "Tetheidae"
- \* several "families" have to be downgraded to subfamily rank (or even to tribe rank): "Phyllocnistidae," "Ethmiidae," "Galleriidae," "Phycitidae," "Pyraustidae," "Lithosiidae," "Ctenuchidae," and so on.

The following section deals with about 30 families, for which are provided keys for the identification of genera and species (pp. 24-1024). For each family, one can find a general diagnosis and at least one illustrated key to species, based on external characters and genitalia. Frequently, there are two separate keys to species (one being based on external characters; the second, on male genitalia), and there may also be a third one, based on female genitalia. In addition, there is a key to genera (or to subfamilies and genera), unless the family contains only one genus in western Russia. By and large, all these keys are more accurate than the one to suborders and families. Although the book is not intended as a taxonomic revision, it provides useful data for each species (e.g., distribution and larval food plants), and includes some interesting proposals or suggestions: *Eretmocera* Zeller, often misplaced in recent literature, is rightly placed within the Scythridae ("Scythrididae"); in the Oecophoridae *sensu auct.*, *Anchinia* Hübner follows immediately *Hypercallia* Stephens, probably because A. L. Lvovsky regards these genera as close relatives, a point of view in agreement with my recent reappraisal of the gelechioid classification (I have transferred both genera to the Elachistidae Hypertrophinae: *Alexanor* 16:239-255); *Uliaria* Dumont is rightly considered a member of the Gelechiidae Dichomerinae (the genus has been occasionally allocated to the "Autostichinae"); etc. Of course, the adopted classification and nomenclature would also require a number of amendments: *Odites* Walsingham is definitely not a member of the Xyloryctidae [see,

e.g., Hodges 1978: *Moths Am. N. of Mexico* 6(1):8–9]; *Millieria* Ragonot belongs to the Choreutidae, not to the Glyphipterigidae (see, e.g., Heppner 1982: *Smithson. Contr. Zool.* 370:1–27); *Phyllonorycter* Hübner must be substituted for *Lithocolletis* Hübner, *Ypsolopha* Latreille for *Ypsolophus* Fabricius, *Lecithocera nigrana* (Duponchel) for *Lecithocera luticornella* (Zeller), and so on.

A list of references (pp. 1025–1041) and an index of Latin names (pp. 1061–1092) conclude the book, along with a list of abbreviations of authors (pp. 1042–1043), and a useful list of botanical names, which gives the correspondence between common and Latin denominations (pp. 1044–1060). The present handbook is highly valuable because it includes a large portion of the European fauna of “Micromoths,” for which no equivalent, recent work has been published up to now. For instance, it takes into account a high percentage of the species known to occur in France: nearly 80% for *Bucculatrix* Zeller, more than 90% for *Caloptilia* Hübner and *Ypsolopha* Latreille, 90% for *Ethmia* Hübner, about 60% for the Scythridae, 93% for the Momphidae, 100% for the Choreutidae, etc.

In conclusion, this work should be included in the private library of any microlepidopterist interested in the Palaearctic fauna. It is to be wished that a similar translation will soon be available for Part Three (dealing chiefly with Pyrales and Plume Moths).

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BUTTERFLY GARDENING IN THE SOUTH: CULTIVATING PLANTS THAT ATTRACT BUTTERFLIES, by Geyata Ajilvsgi. 1990. Taylor Publishing Company, Dallas, Texas. xi + 348 pp., 196 color photographs, 2 line drawings and 7 diagrams. Hard cover, 20.3 cm × 28 cm, ISBN 0-87833-738-5. \$34.95.

Novice and master gardeners in the southern U.S., particularly in the Rio Grande Valley, Texas, have an extraordinary treat in store with this volume. Ms. Ajilvsgi investigates every aspect of a butterfly garden, from her brief introduction on the significance of butterflies and their means of survival to appropriate commercial and private sources for obtaining seed and other garden supplies. The brief forward by Chess Ezzell McKinney, Chairman, Preservation of Butterflies, National State Garden Clubs, sets the stage for this treasury of information, and, although the title focuses on butterfly gardening, the emphasis is on gardening with a capital “G.”

There are special sections of the book devoted to creating a personal butterfly garden and to methods of attracting butterflies, highlighted by personal observations on such topics as the important characteristics of floral nectaries (color, shape and fragrance) and how to choose the appropriate plants, with one of my favorites—adopt a weed. Two other chapters detail the actual planning and planting of a butterfly garden. For the novice, or for butterfly watchers with limited space, there is the “instant” butterfly garden. For example, a fence, porch, or wall can accommodate hanging baskets or vines, and even the edges of driveways or window boxes can function as butterfly gardens. Special attention is given to the selection of plants, maintenance of the garden, and even to the introduction of caterpillars and chrysalids. For those lepidopterists with a grander vision in mind, a series of diagrams (pp. 78–83) provides garden plans for almost any geographic setting in the south. This thorough chapter on planning includes discussions of soils, preparation of the flower beds, and selection of appropriate plants, including native species, in addition to some forethought about flight patterns through the garden and appropriate areas for water and puddling stations. A chapter on “butterfly-friendly pest controls” emphasizes biological and physical controls, companion and repellent plants, and natural insecticides. Butterflies of south Texas, and especially of the Rio Grande

Valley, are featured in the special south Texas garden, which lists local butterflies and their associated larval hostplants based on the current literature and on the author's own field observations.

Detailed analyses for 50 butterfly species that are easily visible in the field or backyard are included and organized according to the common name followed by the scientific name. Each diagnosis generally includes a color illustration, size, range, flight period, number of broods, overwintering stage, and brief descriptions of the adult, egg, and larva, and of the hostplant and parts of the plant consumed. Curiously, descriptions of the chrysalis are omitted. Favorite nectar sources, their bloom period, height class, cultivation, and other notes are also listed. Descriptions of adult behavior, especially favorite perches and interaction with nectar sources, are interspersed throughout this section.

Separate chapters treat larval hostplants and nectar resources, with the plants subdivided according to type (trees, vines, and herbs). These chapters feature both cultivated and native species with a special perspective on south Texas butterflies and with descriptions and accompanying color illustrations for 40 plants in each category. The chapter on larval hostplants provides information on their cultivation, associated larval taxa, and other notes. A longer list of all potential host plants gives the common name of their associated butterflies, the normal plant range, and the geographic area in which these plants are located in Texas (pp. 209–242). Similarly, the chapter on nectar sources lists the most appropriate yet common plants, their habitat association, and identification as a larval hostplant, if appropriate. An addendum list of nectar plants (pp. 281–311), including both cultivated and native naturalized species, is subdivided annuals versus perennials (herb), with special annotation indicating height, color and bloom period.

A wealth of other information can be found in this book, including basic advice and tips on the photography of butterflies. Other features include maps of U.S. hardiness zones and of the regional subdivisions of Texas considered. A compendium of appendices lists the major butterfly and plant organizations and societies and their associated publications, butterfly gardens and special events, and garden magazines and newsletters with articles on butterfly gardening. Other lists provide sources for additional information on habitat preservation, garden seeds, and supplies. The diverse bibliography supplies references on butterflies and other insects; garden, plant and wildflower guides; and photography. The butterfly and plant index is consistent in format, listing species by common name followed by the associated scientific name.

This book is exceedingly well researched and delightfully written. It is refreshing to read the author's personal observations on gardening and butterflies, especially those on behavior. For the taxonomist, the organization of the butterfly diagnoses is a little disconcerting, with, for example, the Janais Patch (*Chlosyne janais*) and the Theona Checkerspot (*Thessalia theona*) interspersed among representatives of the Hesperidae. Similar problems occur in the Lycaenidae.

Although the use of common names as the main reference point may be attractive to introduce the uninitiated gardener to butterflies, such names vary in use from one section of the country to another, leading to confusion. Thus, the Gray Calico and Gray-skirted Calico refer to the same beast, *Hamadryas februa*. One further minor hurdle concerns the type size of the index (6 pt.), which is generally in vogue for curatorial staffs but may be a little small for the average reader.

These few problems notwithstanding, this book is beautifully illustrated and provides a treasury of vital information on butterfly gardening. For anyone even remotely interested in southern gardening and butterflies, this book is absolutely essential reading.

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**BUTTERFLY GARDENING: CREATING SUMMER MAGIC IN YOUR GARDEN**, created by the Xerces Society in association with the Smithsonian Institution. 1990. Sierra Club Books, San Francisco, and National Wildlife Federation, Washington, D.C. xv + 192 pp., 118 color photographs, 4 diagrams. Softcover, 18.5 × 23.5 cm, ISBN 0-87156-615-X. \$18.95.

The cooperative spirit of this volume is reflected not only in the educational and conservation organizations involved in its production, but also by the wealth of individuals—authors, naturalists, and photographers—who so generously donated their time and efforts. *Butterfly Gardening* is dedicated to the broad scale conservation of butterflies and their native food plants. It also celebrates the diversity of nature and encourages all lepidopterists to observe ecology in action. With the loss of native habitats, there also has been a noticeable disappearance of butterfly species, which serve as indicators of major changes in ecosystems.

A brief *Introduction* by Dennis Murphy focuses on some of the problems in butterfly conservation, suggests possible solutions, and sketches the contributions of the other nine authors of the book. Such a conservation approach to butterfly gardening would be incomplete without a contribution from the Honorable Miriam Rothschild, the eminent entomologist who has devoted so much time to the study of butterflies and other invertebrates. Dr. Rothschild's keen insight has made naturalists more aware of conservation and of the significant role of wildflowers in ecosystems. Dr. Rothschild wrote three chapters for this book. The first describes the joys and challenges of *Gardening with Butterflies*; the second explores *The Visual Perception of Lepidoptera* and the importance of providing appropriate nectar sources in butterfly gardens; the third describes *The Life Cycle of the Large White Butterfly*. Some life history aspects crucial to the survival of butterflies and moths in nature—metamorphosis, mate recognition, migration, temperature regulation, natural predators, and defense through camouflage and cryptic coloration and mutualism—are discussed by Dave Winter in his erudite chapter (*The Struggle to Survive*). From a more personal perspective, Jo Brewer recounts her experiences as a butterfly gardener—providing descriptions of some of her more spectacular triumphs, sprinkled with the inevitable problems she encountered (*Notes from a Butterfly Gardener*). She also evaluates the propriety of introducing butterfly species into new habitats and discusses the use of native plant species versus exotic species in butterfly gardens.

Mary Booth, a landscape architect, with supporting text by Melody Mackey Allen, provides butterfly garden designs with emphasis on color. Four basic arrangements from simple to more sophisticated plans are provided and suggestions for flowering plants are included. Some do's and don'ts with regard to conservation and to introduction of plant species that may be difficult to control are also considered. This chapter (*Butterfly Garden Design*) concludes with a master plant list of 30 flowering plants that are common nectar sources and, in some cases, larval hostplants. This annotated list provides a description of the type (shrub versus hardy perennial), height, color, bloom season, exposure, and soil requirements for each species. The food requirements for moths are not neglected owing to the thoughtful inclusion of Dave Winter's chapter on nocturnal nectar sources (*Moths and the Garden at Night*).

Conservation issues concernign habitat are addressed in the chapter *Wildflowers in the Planned Landscape* by David Northington. As the Executive Director of the National Wildflower Research Center, he discusses the disappearance of plants and the resulting ecological consequences for animal species. The poignant discussion by Stanwyn Shetler in *Butterfly Gardening and Conservation* addresses these subjects from a naturalist's viewpoint and delves further into the importance of plant/insect interactions. Dr. Shetler actively supports increased public education and awareness of conservation efforts by promoting gardening to teach preservation, rehabilitation, and restoration of diverse natural habitats.

The final chapters offer suggestions for enhancing personal enjoyment of butterfly



gardens, with excellent tips on close-up photography and butterfly observations by the incomparable Edward Ross (*Enriching Your Personal Landscape* and *Butterfly Photography*) and additional intriguing ideas for butterfly watching by Robert Michael Pyle. Following a short *Afterword* by Pyle are two appendices: a list of nectar plants for North American butterflies and moths and an annotated list of the most familiar North American butterflies and their larval food plants. Resource lists for obtaining garden plants and entomological equipment, a lengthy bibliography, and an index to both scientific and common names complete this useful volume.

An attractive glossy cover adds an exquisite touch to this extraordinarily illustrated volume. Superbly written, this book offers an excellent mixture of conservation philosophy and biological common sense with a focus on butterflies and moths. With such a compilation of authors, the book is anecdotal, and if there is any fault, it is that parts of some chapters may appear redundant. However, such duplicate treatment is refreshing, inasmuch as different perspectives reflect the diversity of thinking on various subjects, such as appropriate nectar sources and problems encountered in rearing species. The Xerces Society and Smithsonian Institution are indeed to be commended for producing this volume. Through conservation, restoration, and management of native habitats initiated at the backyard level, we can increase public awareness of how complex yet fragile nature is and make a new beginning at protecting Lepidoptera.

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THE ONTARIO BUTTERFLY ATLAS, by Anthony M. Holmes, Quimby F. Hess, Ronald R. Tasker, and Alan J. Hanks. 1992. Toronto Entomologists' Association, 34 Seaton Drive, Aurora, Ontario L4G 2K1, Canada. 167 pp., 13 color plates. Soft cover, 20.5 × 25.5 cm, ISBN 0-921631-11-1. Available from the Association for \$29 Canadian (including taxes & p/h) or \$26 U.S. (including p/h) (no Master-Card or Visa).

This attractively covered paper-back culminates the efforts of the Toronto Entomologists' Association (TEA) by recording the skippers and butterflies found in Ontario. The title may be somewhat misleading, however, as this publication is more of an annotated checklist of Ontario Rhopalocera.

The preface, brief author backgrounds, and table of contents are followed by an introduction that describes the purposes of the Atlas: "to summarize . . . the distribution and some characteristics of Ontario butterflies . . . , to encourage . . . others to explore the distribution . . . , and as a reference for planning efforts to conserve . . . rare species. . . ." This introduction also includes information on TEA, nomenclature, timetables, habitat, status (employing symbols of occurrence used by the Nature Conservancy of Canada), records, figures showing counties and districts, physiographic features (Hudson Bay lowlands to deciduous forest region in southwestern Ontario), life zones (Hudsonian, Canadian, Transition and Carolinian), and problem species. The latter category includes several butterflies treated as species by some authors and as subspecies by others; also, because some species of *Erynnis* and *Satyrrium* are difficult to identify, some records may be inaccurate.

The main portion of the *Atlas* treats 138 species, including *Basilarchia arthemis arthemis* and *B. a. astyanax* as separate entities. The authors make no attempt to differentiate subspecies except in a few cases. Each family is introduced with beautiful photographs of adults in natural settings or poses, with the exception of the Hackberry Butterfly on page 111 that suspiciously resembles a pinned specimen!

The authors devote a full page to each species, with brief notes on timetable, including broods and "hibernates," and occurrence, including habitat, food plant, distribution, and

status. Also included on the species page is an occurrence calendar-graph for each stage of the species and a map of Ontario showing distribution by dots placed in each county and district of occurrence. I wish the authors had included more biological information and "characteristics" of each species instead of devoting more than half a page to each distribution map. The 12 color plates include 2 habitat photographs and 27 individual photographs that show 7 larvae and pupa and 20 adults, representing 22 species.

Following the main species section is information on 19 stray species that have been vouchered by a single specimen (e.g., *Erynnis zarucco*) or rarely recorded (e.g., *Speyeria idalia*). It appears to me that these strays should have been included in the main species section, which already includes such strays as *Pyrgus communis*, *Hylephila phyleus*, *Battus philenor*, to name a few. Next is a section listing five unconfirmed species that may range into Ontario based on records from adjacent provinces and Michigan. This section might better have been called a hypothetical species list. The final species section has information on five doubtful species that have been erroneously referred to Ontario as a result of misidentification, improper labelling, or lack of a voucher specimen.

The last four pages of the *Atlas* comprise a bibliography, including check-lists, TEA publications, and general works, and a provincial ranking of status indicating number of occurrences within the province.

This publication is a valuable addition to the literature on Lepidoptera of the region from Hudson Bay to the Great Lakes, although there are a few questionable assertions. For example, the authors state that *Lycaeides melissa samuelis* hibernates "as a larva," but according to James Scott (*The Butterflies of North America*, 1986, Stanford University Press, CA), "eggs hibernate in ssp. *samuelis*..." And for *Danaus plexippus*, the authors mention "positive evidence for a cycle of abundance peaking about every 11 years." In both cases, the authors fail to include literature citations or to otherwise identify the source of this information.

This *Atlas* would have been more valuable if specific rearing experiences and personal food plant observations had been included. Furthermore, there is no discussion under *L. m. samuelis* or other rare or threatened species as to the authors' recommendations of proposed management methods and techniques to preserve or enhance existing populations. This shortcoming appears to be inconsistent with the authors' stated purpose "to provide a reference for planning efforts to conserve our rare species..." Also, I found it interesting that the authors assert that the food plants of *Erynnis persius* are "willows, poplars and aspens." In Michigan, *persius* feeds on lupine and most recent authoritative references state that lupine is the preferred larval food.

The *Ontario Butterfly Atlas*, with an 8 × 10" format, is printed on high quality paper with easy to read type and excellent photographs. I found no typographical errors or improper use of nomenclature. I recommend this publication to all students interested in the butterflies and skippers of Ontario and the Great Lakes region.

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#### OUT OF AFRICA

THE BUTTERFLIES OF KENYA AND THEIR NATURAL HISTORY, by Torben B. Larsen. 1992. Oxford University Press, Oxford, New York and Tokyo. xxii + 490 pp., 19 + A4 figures, 64 color plates. Hard cover, 18 × 25 cm, ISBN 0-19-854011-6. \$195.00.

BUTTERFLIES OF TANZANIA, by Jan Kielland. 1990. Hill House, Melbourne and London. 363 pp., 3 maps, 179 text figures, 68 color plates. Hard cover, 22.5 × 30 cm, no ISBN. \$120.00.

These are two rather comparable volumes devoted to the butterfly fauna of adjacent East African countries. Both are authoritative, even though Kielland's volume represents many more years of sampling the Tanzanian fauna than does Larsen's. Despite this shortcoming, however, Larsen has managed to produce a very readable and useful volume because he has consulted with many authorities and resident Kenyan collectors and has organized the field notes of the latter into an excellent compendium. Kielland's book is no less well-documented and both volumes contain much useful information for either the collector or the butterfly-watcher.

The plates, of course, are the highlight of any butterfly book, and these are of top quality. The specimens illustrated are the best ones available to the authors: those in the Kenya book are presumably the best available at The Natural History Museum, London, whereas the specimens in the Tanzanian book are largely those available in Mr. Kielland's collection, sometimes to the detriment of the Tanzanian work. The larger format of Kielland's book makes possible the life-size illustrations of all taxa. Larsen's book illustrates only half of each spread specimen for larger species and has more reduced figures, but where applicable, this fact is stated on each caption page.

The Kenya volume appears to have been proofread somewhat more stringently than does the Tanzanian one. A number of annoying "typos" in the latter distract the reader. For example, when one seeks the illustration for *Bicyclus kiellandi* Condamin, the plate on which it is figured is stated in the text (page 81) to be Plate 18; the butterfly is actually illustrated in Plate 17! Occasional inappropriate capitalizations of some, but not all, patronymial specific epithets occur throughout the text.

Both books use species citations that do not strictly conform to the *Rules of Zoological Nomenclature* because they do not place the authors' names in parentheses when a species or subspecies was described in a genus other than the one in which it is presently contained. This habit, while maddening to the purist, seems to be gaining acceptance among authors, and perhaps it will no longer be required in future *Rules*.

Larsen is a superb writer who manages to use humor to its greatest advantage. He does not always write humorously, but rather interjects it occasionally. For example, on page 34, during a discussion of urine being attractive to butterflies, he provides this aside: "(When collecting in the tropics I often take a couple of Johnnie Walker bottles full of urine with me; whoever once stole two such bottles from my car must have been in for a surprise when he reached home)." I suspect that there is more useful information about habits of butterflies in the Kenya book, but both provide much useful data.

I have only two major criticisms, neither perhaps important in itself, but both of which are an annoyance. Both books contain a number of descriptions of new taxa, especially in the Kielland book, which make the books indispensable to the taxonomist. There seems to be a "conspiracy" on the part of some authors to include such descriptions in books to enhance sales, but perhaps this not intentional. Steve Collins and Larsen do describe their new species in an appendix (pp. 438-445) almost apologetically, which seems to mitigate my objection mentioned above. Kielland does not so segregate his new names (as well as those of other authors), which are included throughout the text. Type specimens are illustrated in both books, thereby further increasing their utility to the specialist.

The second criticism applies only to the Kielland book, and it is not the author's fault: the type faces employed throughout the book are so similar to one another (family-group names are in slightly larger type) that it is extremely difficult to locate information quickly or determine where one discussion ends and the next begins. In Larsen's book, the main headings are much better accentuated, and one can tell at a glance what constitutes any species discussion. In addition, genera are well separated in that text, whereas in the Tanzanian volume there is no difference in typography between genera, species or subspecies.

These are really minor complaints, however, and both books are significant additions to the African butterfly literature. They are well-written and superbly illustrated, and though both volumes are somewhat expensive, they are well worth the money. If the reader has to choose only one of the volumes (they do cover roughly the same fauna of nearly 900 butterfly species), I would have to recommend Larsen's volume over Kielland's based chiefly on the clarity of the former's presentation. Hopefully, no one will have to

choose and those interested in east African butterflies can have both volumes—the authors are to be congratulated for their accomplishments.

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A PRACTICAL GUIDE TO BUTTERFLIES AND MOTHS IN SOUTHERN AFRICA, by S. E. Woodhall (co-ordinating editor) et al. 1992. Lepidopterists' Society of Southern Africa, P.O. Box 470, Florida Hills, 1710, Transvaal, Republic of South Africa [Sponsored by Monsanto South Africa (Pvt) Ltd., Agricultural Group]. 223 pp., 48 color photographs on 8 plates, numerous black and white photographs and text figures. Softcover, glossy paper, 14.5 × 21 cm, ISBN 0-620-16774-2. Available from the Lep. Soc. So. Africa for \$25 U.S. plus postage (\$1 for surface mail or \$20 for Airmail).

This techniques guide was compiled through the efforts of nineteen of the top lepidopterists in southern Africa. It is an easily totable resource (approximately 6" × 8" × ½") for almost every aspect of studying Lepidoptera, meant for use by beginners as well as by others who desire to learn more about techniques used in other countries. It is easy reading, even amusing at times, and the techniques appropriate for southern Africa are certainly usable here. Although the price is high for a paperback, the book is absolutely stuffed with information!

Chapter topics include the history of lepidopterists and lepidopterology in southern Africa, the lepidopteran life cycle, morphology and terminology, binomial nomenclature, species theory, evolution of Lepidoptera, a discussion on "lumpers vs. splitters," taxonomic classification, and the rules that govern scientific nomenclature (ICZN). As expected in a work meant to address beginners, the book is amply illustrated with black and white photographs, line drawings, cartoons, and eight pages of color photographs depicting 48 live specimens of butterflies, moths (even some micros), and larvae which accompany the systematic classification of Lepidoptera and a brief overview of Lepidoptera.

A chapter devoted to Lepidoptera conservation in southern Africa presents the various habitat changes and impacts that man's activities have had on insect populations and includes discussions of monitoring methods (conducting mark-recapture studies, hostplant monitoring, habitat monitoring). Also in this chapter is mention of the *South African Red Data Book—Butterflies*, a publication documenting 102 species considered to be exposed to some level of threat. This guide provides a table of 190 or so rare, endangered or vulnerable butterfly species cross tabulated with habitat, habits, distribution, taxonomy, food, and reproduction. Checkmarks in the columns denote a *lack of information* about a specific aspect of the particular butterfly. This table draws attention to those aspects unknown, with the idea that special efforts should be made to remedy these "unknowns."

Collecting and field techniques for butterflies are detailed and are accompanied by photographs, cartoons, and line drawings. Included are instructions on the construction of equipment and the proper use of nets, traps, decoys and baits, killing methods, and specimen storage in the field, along with suggestions for observing hilltopping, territoriality, and egg laying behavior. Especially interesting are the instructions for preparing rotten shrimp bait, various fruit baits, and different combinations of scat and urine to attract specimens. Apparently, the fresher the dung, the better (baitwise). However, a cautionary note is included to remind the lepidopterist to keep a sharp lookout for the originator of the dung; e.g., lions, elephants, baboons, etc. Discussion of moth collecting includes traps (many diagrams and photos), sugaring, and the collecting of immatures.

Preservation and mounting techniques are covered thoroughly. Relaxing techniques (chambers, injection, cutting wing muscles), selecting pin sizes, pinning specimens, con-

struction of various spreading boards, use of various materials as "setting strips," and setting pins are all discussed. The actual spreading technique for butterflies and macros is described in detail, with many cautions included for the inexperienced. There are also instructions for baking (=drying) specimens while on the spreading board. Although the description of techniques for pinning micros is brief, detailed instructions are given for preserving and mounting early stages, and for dissection and preservation of genitalia, palpi, legs, androconia, and larval head shields. Degreasing, dust removal, mold removal, repairing damaged specimens, housing the collection, prevention of infestation, proper labelling, and hints for successful mailing of specimens are also included in this chapter.

Other topics covered in this guide include rearing and breeding Lepidoptera (cages, sleeving, foodplants, artificial diets, and larval diseases) and photography in the field and in the studio (backdrops and composition, as well as proper storage of photographs). There are chapters on good scientific practice, the British Butterfly Conservation Society Code of Practice, several appendices (providing addresses of equipment dealers, names and addresses of journals worldwide that accept Lepidoptera papers, reviews of threatened species in southern Africa), a glossary of terms, a bibliography, and an index.

Throughout the book the authors encourage all lepidopterists to expand and further the science of lepidopterology. Emphasis on observations in the field and the elucidation of life histories are recurring themes in this handbook that espouses a common-sense approach to the study of Lepidoptera. Amateur lepidopterists are hailed for tirelessly providing valuable information, continually taking on the onerous task of breeding and recording life histories, and contributing much of what is known about Lepidoptera. The debate over collecting vs. no-collecting is broached. Admitting that it is an emotionally charged issue, the authors agree that general bans on collecting are detrimental to the conservation of Lepidoptera and of nature as a whole. Conservation is promoted and responsible collecting is encouraged. The point is made that the reproductive capabilities of insects far outweigh the impact of the small numbers collected by lepidopterists. A reminder to all is that the younger generation should be encouraged to study invertebrates; that first-hand collecting and field experiences, besides being enjoyable, entice children to become more aware of nature and more able at a later date to make informed judgements on conservation matters; and that if "... no more children are starting at the basics, one day there will be no lepidopterists to be consulted on conservation."

I found the book to be an inspiring and complete guide to handling Lepidoptera, written in an easy to understand, often entertaining manner. It was rewarding to read a techniques book that continually encouraged and lauded the efforts of avocational lepidopterists. It sets an excellent example for our own future *Lepidopterists' Society Techniques Manual*.

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## MANUSCRIPT REVIEWERS, 1993

The merit of a scientific journal depends on the quality of its reviewers as well as of its authors, but the former are usually unknown to readers. The *Journal* relied on the expertise of 68 reviewers last year to provide 89 evaluations of manuscripts. It is with much gratitude that the *Journal* acknowledges the services of the people listed below from whom manuscript reviews were received in 1993.

Phil R. Ackery, London, England  
Annette Aiello, Panama  
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**Cover illustration:** The buckeye butterfly (*Junonia coenia*) is a common and widespread species of North America. Original drawing by Marianne C. Filbert, P.O. Box 155, Logan, Utah 84321.

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## SAMPLING STRATEGIES FOR ESTIMATING MOTH SPECIES DIVERSITY USING A LIGHT TRAP IN A NORTHEASTERN SOFTWOOD FOREST

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**ABSTRACT.** A 22-watt black-light trap was operated for 29 nights within a forest canopy in the Maritime Lowlands Ecoregion of the Acadian Forest. The species-abundance frequency distribution (pattern of species abundance) was a good fit to the log series model and this model was used for subsequent data analysis. No single-night sample adequately estimated the log series *alpha* index of diversity based on the total catch; some sampling effort was required each night. Each night's catch was separated into 16, 30-minute samples. The *alpha* index of diversity for the summed catch for each time-period was compared with the overall *alpha* based on the total catch. A strategy that involved operating the trap for just a 1-hour period each night had no effect on the pattern of species abundance and gave a value for *alpha* equal to that obtained by operating the trap for an 8-hour period each night. This strategy reduced the catch from 6088 to 971 moths and the number of species from 255 to 161. Processing costs associated with the larger sample and any possible negative effect on the moth population caused by removal trapping were greatly reduced. This new sampling strategy is thus useful for comparing indices of species diversity between several sites when data are collected simultaneously, but is of limited use for species-inventory studies.

**Additional key words:** species-abundance distribution, 30-minute samples, log-series model, partial-night sampling.

In recent years, the challenge to maintain biodiversity on this planet has become a major public concern. Most attention focuses on Neotropical ecosystems (Mares 1992). However, the importance of maintaining Canada's biodiversity was addressed in Environment Canada's Green Plan (Hyslop & Brunton 1991), and the launching, in 1991, of "Canadian Biodiversity" produced by the Canadian Centre of Biodiversity at the Canadian Museum of Nature lends credence to the recent

national interest in biodiversity. The values of maintaining current biodiversity have been stated by many authors, and summarized by Ehrlich (1990) into ethical, aesthetic, economic, and 'ecosystem services.' Salwasser (1990) added the legal obligation for conserving biological diversity. Intimately linked with the concept of maintaining biodiversity, and especially protection of areas rich in species, is the need for a "quick and dirty survey to chart biodiversity of the planet" (Roberts 1988), a view reiterated by Ehrlich (1992). The 'quick and dirty' approach does not advocate poor science; rather, it recognizes that the scope of diversity from individual gene systems through populations of species, communities, ecosystems, and ultimately all life in the biosphere (Wilson 1988) cannot be addressed in the short-term. It suggests that studies should be focused on certain taxonomic groups over an extensive area. The hope is that areas with many species or high endemism in the selected groups will reflect similarly high values for other groups (Roberts 1988). Because of logistic and knowledge constraints, the number of species within a community can be determined for only a limited number of taxonomic groups.

This study addresses just one segment of biodiversity, i.e., the diversity of moths in a single ecosystem. Diversity is used here to mean the number of species and their relative abundance (Magurran 1988), and to prevent ambiguity we will always use 'species diversity' where appropriate. Relative abundance is considered in the form of species-abundance frequency distributions, which show the relationship between the abundance of individuals and the number of species possessing that abundance (May 1975); abbreviated in this paper as the pattern of species abundance. The ecosystem studied is one locality in the Maritime Lowlands Ecoregion of the Acadian Forest (Loucks 1962).

The use of the moth community, in the 15 families used in this study (see Appendix), as an exemplar of the species diversity of this ecosystem has advantages that include the relative ease of identification at the species level, the somewhat standardized sampling methodology (Williams 1951, Williams et al. 1955, Taylor & French 1974, Bowden 1982), and the high correlation of insects, in general, with the spatial, architectural, and taxonomic diversity of plants (Southwood et al. 1979).

No community consists of species of equal abundance (Magurran 1988). It is normally the case that the majority of species are rare while a number are moderately common with the remaining few species being very abundant (Williams 1964, May 1975, Pielou 1975, Southwood 1978, Magurran 1988). Within this general distributional form, communities have characteristically different patterns of species abundance which remain stable despite changes in species composition (Pielou 1975, May 1976, Kempton 1979). The pattern of species abundances

at a site allows for comparison with similar sites that have different mixes of species, and a change in the pattern of abundance at one site has been shown to be a useful indicator of environmental disturbance (Kempton & Taylor 1974, Taylor et al. 1978, Kempton 1979).

Four main species-abundance models (the geometric series, the logarithmic series, the log normal distribution, and MacArthur's broken stick model) have been developed to describe species diversity in terms of an 'index parameter' as well as the pattern of species abundance. In addition there are several non-parametric indices based on the proportional abundances of species (May 1975, Southwood 1978, Magurran 1988).

The log series model was the first to describe the pattern of species abundance (Fisher 1943). Since then it has been found to have a wide application for catches of many invertebrates, e.g., moths in light traps (Williams 1943, 1945, 1964, Taylor & Brown 1972, Taylor & French 1974, Kempton & Taylor 1974, Taylor et al. 1976, 1978, Taylor 1986), Ichneumonidae (Owen & Chanter 1970), cockroaches (Wolda 1983), Psocoptera (Broadhead & Wolda 1985), Hymenoptera (Noyes 1989), and the community of phytophagous arthropods on apple (Brown & Adler 1989). Its wide applicability is because it is based on the abundances of the species with medium abundance rather than the very abundant and very rare species (Taylor et al. 1976, Kempton 1979, Brown & Adler 1989).

The log series is a simple two-parameter model, with two defining multispecies population parameters, *chi* and *alpha*. *Chi* is devoted to sample characteristics and varies with sample size as it is a function of the mean number of individuals per species. *Alpha* is independent of sample size and characterizes the required population quality (Kempton & Taylor 1974). Fisher's (1943) initial suggestion was that *alpha* might be useful as a measure of 'species richness' when comparing samples. Williams (1943) suggested that the parameter *alpha* be known as a community's 'index of diversity.' Later he recognized that this term was applicable to other functions having the same properties and referred to Fisher's *alpha* as 'diversity calculated on the basis of the logarithmic series' (Williams 1964). The log series model can be derived from two statistics, *S*, the total number of species, and *N*, the total number of moths. It is a discontinuous frequency series with an infinite number of terms:

$$n_1, n_1\chi/2, n_1\chi^2/3, n_1\chi^3/4, \dots,$$

where  $n_1$  is the number of species with 1 individual and successive terms with 2, 3, 4, etc. individuals, and  $\chi$  (*chi*) is a constant  $< 1$  (Williams 1947).

The log normal model was compared with the log series model by Kempton and Taylor (1974) in an analysis of moth catches from light traps at 18 sites for four successive years in an attempt to quantify intuitively recognized properties of habitats. This comparison found that samples from stable environments were best fitted by the log series whereas those from highly perturbed sites better fitted the log normal. Their overall conclusion was that *alpha* of the log series was the superior diversity discriminant, which they defined as a population parameter that behaves consistently within a stable population and responds to changes within, and to differences between, environments (see also Taylor et al. 1976).

The Simpson-Yule diversity statistic and the Shannon-Weaver information statistic (both non-parametric indices) were compared to the log series *alpha* index of diversity by Taylor et al. (1976) using 10 years of light-trap data at one site. Although the log series model was not the ideal description of the pattern of species abundance, the site's environmental stability was better reflected by *alpha* than by either of the other two statistics.

One constraint with using the moth community as an exemplar of species diversity for an ecosystem is the logistics of sorting, counting, and identifying all the individuals in the sample (Taylor 1979). For example, a one-night catch from one trap in Kenya exceeded 6.7 kg (Taylor et al. 1979); 26,300 moths were captured in one light-trap during a nine-month period at Rothamsted (UK) (Williams 1964); 113,256 moths were taken in one light-trap in one year in Kansas (USA) (Williams 1945); 6088 moths were taken in one trap in one month (this study). Methods for reducing the size of catches were detailed by Taylor and Brown (1972), and for subsampling from large catches by Taylor et al. (1979). The objectives of this study were: (1) to describe the species-abundance frequency distribution and determine the log series *alpha* index of diversity, for moths captured in a light-trap in a within-canopy site of a predominantly balsam fir forest during the flight season of the major forest pest, spruce budworm (*Choristoneura fumiferana* (Clemens) (Tortricidae)), and (2) to develop a sampling strategy that reduced the catch to a minimum without causing significant loss of information, measured as no change in the pattern of species abundance and a reduction in the *alpha* value of 5% or less.

## METHODS

**Moth collection and identification.** Beginning on 21 June 1990 (day 1) and ending on 30 July (day 40), one 22-watt black-light trap (Universal Light Trap, Bioquip Products, California) was operated in the Peter Brook study area of the Acadia Forest Experiment Station near

Fredericton, New Brunswick, Canada. For a variety of reasons, full-night trap data are available for only 29 of the potential 40 nights. Intensive studies on the population dynamics of spruce budworm have been in progress at this site since 1986. The physical characteristics and vegetation of the site have been described (Lethiecq & Regnière 1988). Briefly, the study area is composed of 77% balsam fir, *Abies balsamea* (L.) Miller (Pinaceae), 12% red maple, *Acer rubrum* L. (Aceraceae), and eight other tree species. However, the surrounding area is heterogeneous and within a 10-km radius contains mixed forest, lakes, streams, sphagnum bogs, large clear-cuts, and roadsides.

The trap, with the lamp at 6.4 m above the ground, was on a platform, 3 × 1.5 m, on a tower within the closed crowns of balsam fir trees; the otherwise touching branches were trimmed to leave a clearing of 3 × 1.5 m. A blue plastic sheet, 1.8 × 2.4 m, was stretched above the platform at a height of 2.4 m above the lamp. This sheet made direct observation of the light impossible from above, although the reflection of the light off of the foliage of the adjacent trees gave a glow to the immediate area which was obvious from the ground.

The trap was equipped with an automatic time-interval collecting device (King et al. 1965, Smith et al. 1973). Each night's total catch consisted of 16, 30-minute sequential samples, beginning with time-period 1 from 2130–2200 h and ending with time-period 16 from 0500–0530 h. On 21 June, day 1, sunset was at 2120 h and sunrise the following morning at 0536 h; on 30 July, day 29, sunset was at 2058 h and sunrise the following morning at 0606 h. At the latitude of New Brunswick, the sky is noticeably lighter about 30 min before sunrise and remains light for 30 min after sunset.

The moths were killed with 1,1,1 trichloroethane. Moths were stored at –17°C until identified and counted. Most specimens were identified with the aid of the literature and confirmed by consulting the Forest Insect and Disease Survey (FIDS) Reference Collection, Canadian Forest Service, Fredericton, which contains specimens identified by the Biological Resources Division (BRD) of the Centre for Land and Biological Resources Research, Ottawa. Genitalia mounts of specimens were made when identification was uncertain. A further 52 species of geometrids were identified by Klaus Bolte and 81 species of noctuids by Don Lafontaine, both at BRD. All moths in the following families were identified to species and counted: Hepialidae; Sesiidae; Cossidae; Limacodidae; Thyatiridae; Drepanidae; Geometridae, except for *Eupithecia*; Lasiocampidae; Saturniidae; Sphingidae; Notodontidae; Arctiidae; Lymantriidae; and Noctuidae. In addition, all specimens of spruce budworm (Tortricidae) were counted. Moths belonging to other families were not identified or recorded. Publications used for species identi-

fication were Forbes (1954), McGuffin (1967, 1972, 1977, 1981), Rockburne and Lafontaine (1976), Ferguson (1978), Morris (1980), McCabe (1980), Covell (1984), Laplante (1985), Lafontaine (1987), and Lafontaine and Poole (1991).

**Species-abundance frequency distribution.** The numbers of species having abundances of 1, 2, 3, . . . , 724 moths (based on the total catch) were compared with the expected numbers from the log series model (Williams 1947) for goodness-of-fit, using the *chi*-square test (Owen & Chanter 1970, Kempton & Taylor 1974, Taylor et al. 1976, Broadhead & Wolda 1985, Magurran 1988, Noyes 1989, Basset & Kitching 1991). The observed abundances covered a large range, 1–724 moths per species, and because many of these 724 abundance classes were zero (e.g., abundance classes 31 and 36 each had two species, but no species had just 32, 33, 34, or 35 moths and thus classes 32–35 were zeros) the abundance classes were grouped into 10 new abundance classes of approximately equal range on the logarithmic (base 2) scale (Kempton & Taylor 1974, Kempton 1975, Taylor et al. 1976). Because the abundance class having >511 moths had an expected frequency of <1 species, this class was pooled with the preceding class to give an expected frequency of >1 species; resulting in just nine abundance classes. This grouping and pooling of abundance classes (see Table 2) resulted in the data set meeting the requirements for the *chi*-square analysis in that no more than 20% of the classes had an expected frequency of <5 species (1 out of 9 did) and no expected frequency was <1 (Zar 1984).

**Index of diversity.** For the purpose of this study, the 29-night sample from the trap was taken to be the population being sampled. The log series *alpha* index of diversity was determined after rearranging equations (7) and (8) of Williams (1947) to obtain:

$$[1] \quad (Sx / -\ln(1 - x)) - N(1 - x) = 0$$

and solving for  $x$  using MathCad (1991), and then solving [2] for *alpha*:

$$[2] \quad \alpha = N(1 - x) / x$$

This value based on the single 29-night sample was termed 'the overall *alpha*.'

**Strategies to reduce sample size.** Three data manipulations were employed to determine a strategy that would reduce the size of the sample and thus reduce processing costs and lessen the possible effect of removal trapping on the moth population.

**Single-night samples.** The first attempt at a sampling strategy was to determine *alpha* for each night's catch and to compare each value with the overall *alpha*. Such a strategy would certainly reduce sample size, but it was not known how representative such an *alpha* based on



one night's catch would be of the overall *alpha* based on the total 29-day catch.

**'Replicated' single-time-period samples.** As each night's catch consisted of 16 sequential 30-minute samples, there were 16 single-time-period samples, with each sample 'replicated' for 29 nights. The *alpha* index of diversity was calculated for each pooled time period (e.g., all the moths trapped during time period 1 were pooled) and compared with the overall *alpha*. If an index equivalent to the overall index could be estimated from a single 30-minute sample taken each night for 29 nights, significant saving in processing costs would occur, i.e.,  $1 \times 29 = 29$  samples instead of  $16 \times 29 = 464$ .

**Truncated samples.** This strategy was based on the results of the single-time-period analysis. As certain time periods gave low *alpha* values, it was argued that these time periods could be eliminated (thus reducing the number of samples, the number of moths, the processing costs) without significant loss of information. Two sub-strategies were employed. The first, termed **early truncation**, was to discard cumulative sequential time periods from the entire data set beginning with all 29 samples from time period 1, then all 58 samples from time period 1 + time period 2, etc. After 15 truncations only the data set from time period 16 remained. The *alpha* index of diversity was calculated from the data set remaining after each truncation and compared with the overall *alpha* to determine the percentage change. Also after each truncation, the pattern of species abundance was compared with that from the log series model using the deviance *chi*-square values (Kemp-ton & Taylor 1974). The second sub-strategy, termed **late truncation**, was similar to early truncation except that all 29 samples from time period 16 were first discarded, then all 58 samples from time periods 16 + 15, etc. Combining selected data sets that remained after early and late truncation (effectively a **double-ended truncation**) gave several sampling strategies that met the goal of reducing sample size without compromising the value for *alpha* or the pattern of species abundance. The durations for these sampling strategies are shown in Table 1.

## RESULTS

Totals of 6088 individual moths representing 255 macrolepidoptera species in 15 families were identified from the 29-night catch (see Appendix).

**Species-abundance distribution and index of diversity.** The pattern of species abundance is shown in Table 2. In general, the number of species in the abundance classes decreased as the abundance increased. Most species (52) were in the first abundance class, making this the

TABLE 1. Time-periods for sampling strategies.

Strategy #	Inclusive time-periods	Extent of sample (h)
1	1-16	2130-0530
2	3-10	2230-0230
3	3-9	2230-0200
4	4-10	2300-0230
5	4-9	2300-0200
6	5-10	2330-0230
7	5-9	2330-0200
8	6-10	2400-0230
9	6-9	2400-0200
10	7-10	0030-0230
11	7-9	0030-0200
12	8-10	0100-0230
13	8-9	0100-0200
14	9-10	0130-0230

commonest class. The apparent paradox is that members of these species were rare with just one moth in each species (see Appendix). The fewest species (3) were in the largest abundance class making this the rarest class but members of these species were abundant (>255 moths in each, see Appendix). Also shown in Table 2 are the frequencies expected from the log series model. The similarity between observed and expected appears close and is confirmed as being a good fit by the deviance *chi*-square value of 8.6. The 5% critical value of the *chi*-square distribution with 7 df is 14.1 indicating that the log series model provides a good description of the data. The overall *alpha* index of diversity was 54.

**Single-night samples.** The number of moth species and individuals trapped in a single night ranged from a low value of 30 moths in 18 species to a high value of 548 moths in 88 species. Values for *alpha*

TABLE 2. Species abundance frequency distribution of a moth catch in the Acadia Forest Experiment Station compared with expected frequencies from the log series model.

Individuals per species	Number of species		Chi-square
	Observed	Expected	
1	52	53.4	0.04
2-3	47	43.9	0.22
4-7	42	39	0.23
8-15	36	35.4	0.01
16-31	37	31.3	1.04
32-63	22	25.3	0.43
64-127	7	16.9	5.80
128-255	9	7.8	0.18
256-511	2	1.76	1.87
512+	1	0.11	

Total *chi*-square = 8.6,  $P < 0.5$ ,  $P > 0.1$ ,  $df = 7$ . Last abundance class pooled with previous class to meet requirements of *chi*-square test (see Methods).

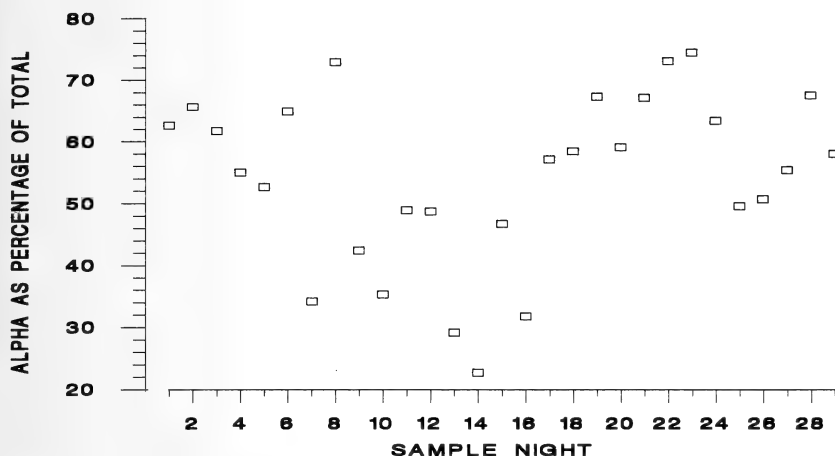


FIG. 1. *Alpha* index of diversity for single-night catches as a percentage of the overall *alpha* based on the total catch.

fluctuated wildly between 12 and 40 with no meaningful trend and never closely approaching the overall *alpha* (Fig. 1). It was apparent that no single-night sample could be used to estimate the index of diversity and thus no pattern of species abundance was determined.

**'Replicated' single-time-period samples.** For any single 'replicated' time period (consisting of 29, 30-minute samples) the total number of moths trapped ranged between 48 and 627 and the total number of

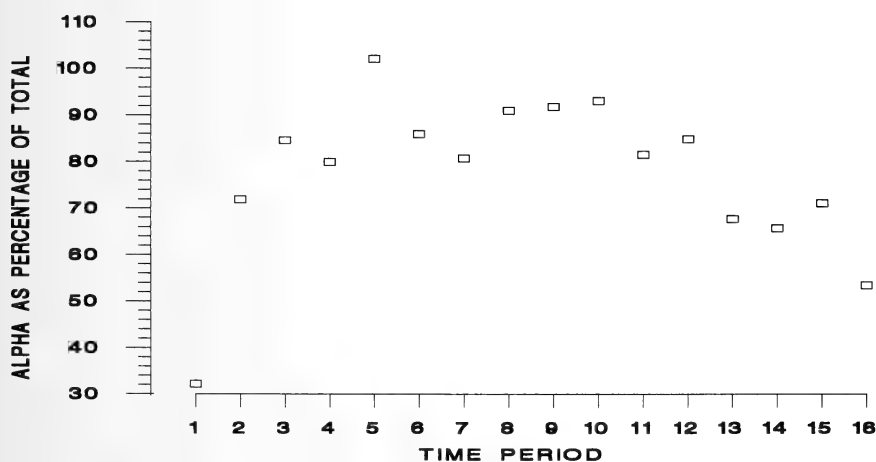


FIG. 2. *Alpha* index of diversity for single-time-period catches, averaged over 29 nights, as a percentage of overall *alpha* based on the total catch. Time periods are sequential 30-minute periods starting at 2130–2200 h and ending at 0500–0530 h.

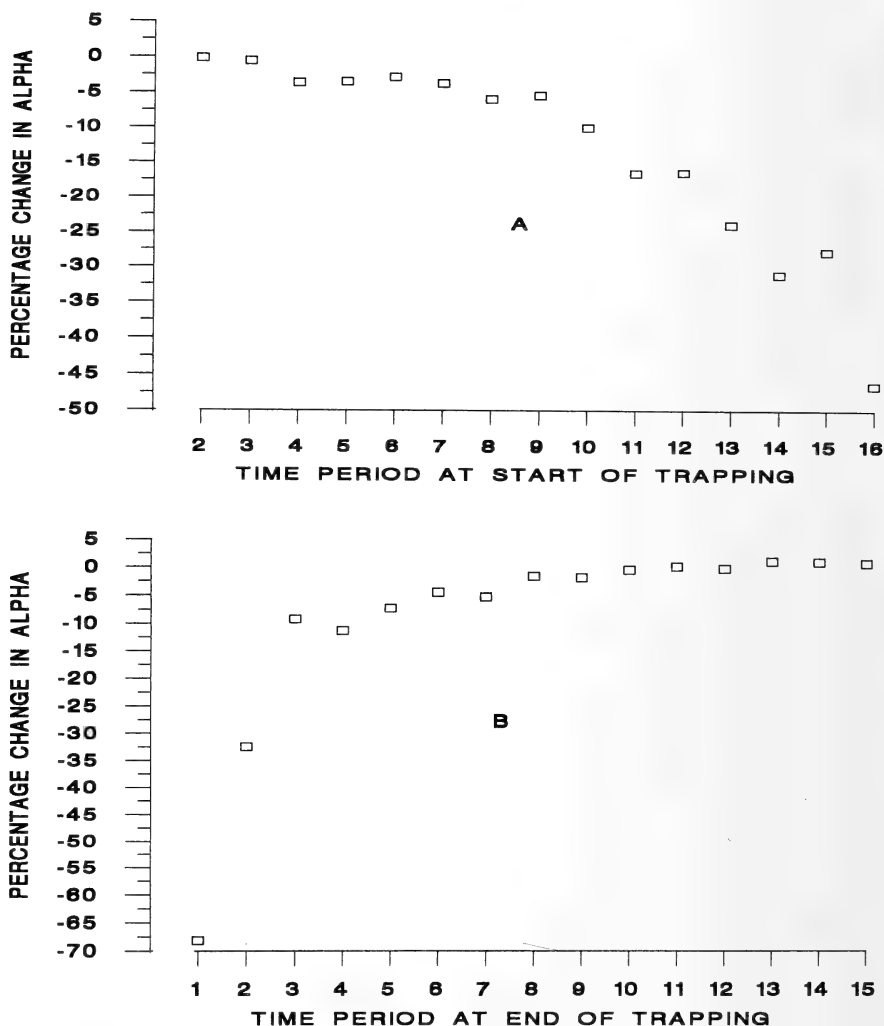


FIG. 3. Percentage change in the *alpha* index of diversity compared to the overall *alpha*: (A) when trapping starts with successively later time periods and ends with time period 16 (0500–0530 h); (B) when trapping starts at time period 1 (2130–2200 h) and end at successively later time periods.

species trapped ranged between 23 and 132. The values for *alpha* for the 'replicated' single-time-period samples started low in the first part of the night, rose rapidly to a maximum during the middle part of the night and then decreased towards dawn (Fig. 2). For time period 5 the value for *alpha* was 102% that of the overall *alpha*. However, this datum was an outlier that did not follow the trend and it was not thought

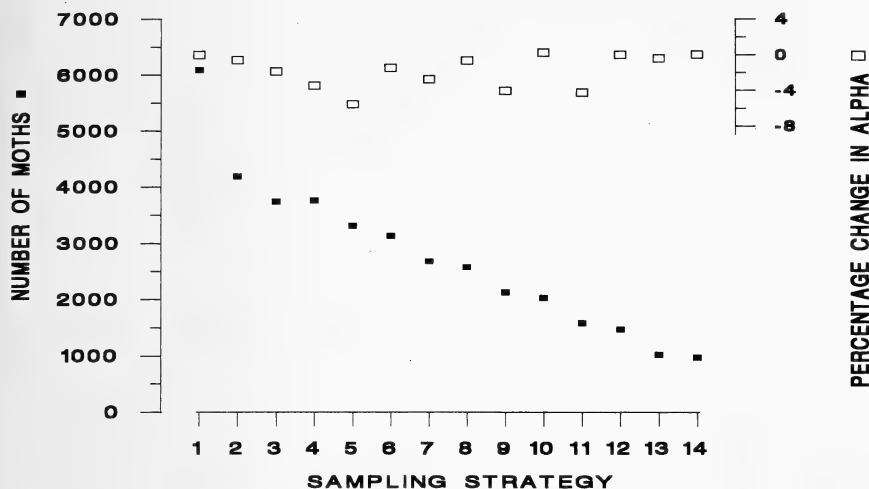


FIG. 4. Percentage change (empty rectangles) in the *alpha* index of diversity relative to the overall *alpha* (strategy 1), and number of moths trapped (solid rectangles) for the various sampling strategies. See methods and Table 1 for explanation of sampling strategies.

prudent to accept this single time period as representative of the overall *alpha*.

**Truncated samples—early truncation.** Discarding the data in time periods 1 through 6 had no significant effect on *alpha* determined from the remaining data set (Fig. 3A). That is, if the light trap had begun operating at 0030 h, start of period 7, and had run until 0530, *alpha* would have been within 5% of the value obtained by starting the light trap at 2130 h. Also, early truncation of time periods 1 through 6 had no effect on the pattern of species abundance in the remaining data set (time-periods 7–16), *chi*-square = 10.2, 7 df ( $P > 0.1$ ).

**Late truncation.** Discarding the data in time periods 16 through 9 had no significant effect on *alpha* based on the remaining data set (Fig. 3B). That is, if the light trap had begun operating at 2130 h and had run until 0130 h, the end of period 8, *alpha* would have been within 5% of the overall *alpha*. Also, late truncation had no effect on the pattern of species abundance in the remaining data set (time periods 1–8), *chi*-square = 7.7, 6 df ( $P > 0.1$ ).

**Double-ended truncation.** Several combinations of early- and late-truncation provided 13 sampling strategies that reduced the sampling period and reduced the number of moths trapped. These strategies (Table 1) had no significant effect on *alpha* and did not compromise the pattern of species abundance. No calculated *chi*-square value, comparison between observed pattern of species abundance and expected

pattern from the log series model, was significant ( $P > 0.05$ ). When the sampling strategies were arranged in a sequence of decreasing sampling periods (Fig. 4), the downward trend in the number of moths trapped and the insignificant effect on *alpha* became obvious. The most cost-effective strategy was a 1-h sample obtained nightly from 0130–0230 h (strategy 14, Fig. 4) that resulted in a total sample of 971 moths in 161 species giving an *alpha* value of 55.

### DISCUSSION

The inadequacy of a single-night sample to estimate accurately the *alpha* index of diversity for moths caught during a one-month period was observed by Williams (1943, 1964) in England. Nightly samples during the month of July gave *alpha* values that varied from 42–81% of the overall *alpha* based on the total catch for the whole month, with no evidence of any regular trend (Williams 1964, Table 67). Taylor and Brown (1972) presented data from two traps for nine days in July in Kenya. Single-night *alpha* values ranged from 30.5–80% of the two overall values. Our data showed a similar random pattern with nightly values varying from 22–74% of the overall *alpha* value. Even when Williams (1964, Table 67) calculated diversity on a weekly basis, the average weekly value for *alpha* was only 77% of the monthly value. These data support our conclusion that some sampling effort is required nightly throughout the duration of the calendar dates of interest.

Taylor (1979) commented on the cost-efficiency of sampling insects and the advantages of an attractant trap, such as a light trap, in selecting specific taxa. He also noted that, when used to control pest-species, light traps have as an objective the removal of as large a proportion of the population as possible. However, when used as a monitoring tool, the objective is to affect the population as little as possible compatible with obtaining adequate numbers for analysis. As mentioned in the introduction, large samples have problems associated with the cost of sorting, identifying, counting, and data handling. Reducing sample size by subsampling from a larger sample has drawbacks (Taylor et al. 1979). Taylor and Brown (1972) tried several methods to decrease the size of the moth catch in light traps that included obscuring the light with black paint, changing the source of illumination (different bulb types), and changing the direction of illumination. These methods reduced the size of the catch, but had no effect on the *alpha* index of diversity. They did not examine the effect on the pattern of species abundance.

Our technique of a short-time-period 'replicated' nightly sample to determine the *alpha* index of diversity without changing the pattern of species-abundance is new. Because it results in a relatively small sample, it has the advantage of affecting the moth population much

less than a full-night sample. It appears to be of use for determining the moth species diversity of several sites simultaneously which otherwise could not be considered because of processing costs associated with the usually large catches in light traps.

There are no *alpha* index of diversity values from eastern North American forests in similar latitudes with which to compare the *alpha* value obtained in this study. The long-recognized latitudinal and longitudinal gradients in species diversity (Pianka 1966, Smith 1980, see also refs. in Magurran 1988) preclude comparison of the *alpha* value from this study with *alpha* values for moth species diversity in two mid-west American states (Williams 1945) and England (Taylor et al. 1978).

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## APPENDIX. Species list with numbers of moths and extreme dates of capture.

<b>Hepialidae</b>		
<i>Korscheltellus gracilis</i> (Grt.)	23-24 July	3
<b>Sesiidae</b>		
<i>Synanthedon acerni</i> (Clem.)	25 June-24 July	11
<b>Cossidae</b>		
<i>Prionoxystus macmurtrei</i> (Guer.)	28 June	1
<b>Tortricidae</b>		
<i>Choristoneura fumiferana</i> (Clem.)	2-29 July	450
<b>Limacodidae</b>		
<i>Tortricidia testacea</i> Pack.	26 June-4 July	4
<i>Tortricidia flexuosa</i> (Grt.)	25 June-29 July	40
<i>Packardia geminata</i> (Pack.)	21 June-29 July	13
<i>Lithacodes fasciola</i> (H.-S.)	26 June-21 July	7
<b>Thyatiridae</b>		
<i>Habrosyne scripta</i> (Gosse)	25 June-18 July	3
<b>Drepanidae</b>		
<i>Drepana arcuata</i> Wlk.	21 June-21 July	20
<i>Drepana bilineata</i> (Pack.)	26 June-29 July	25
<i>Oreta rosea</i> (Wlk.)	10-29 July	5
<b>Geometridae</b>		
<i>Protitame virginalis</i> (Hulst)	21 June-22 July	9
<i>Itame pustularia</i> (Gn.)	14-29 July	183
<i>Itame brunneata</i> (Thunb.)	25 June-17 July	2
<i>Itame anataria</i> (Swett)	17 July	1
<i>Semiothisa aemulataria</i> (Wlk.)	19 July	1
<i>Semiothisa ulsterata</i> (Pears.)	29 June	1
<i>Semiothisa transitaria</i> (Wlk.)	18 July	1
<i>Semiothisa minorata</i> (Pack.)	21 June-29 July	17
<i>Semiothisa bicolorata</i> (F.)	16-19 July	4
<i>Semiothisa bisignata</i> (Wlk.)	29 June-19 July	8
<i>Semiothisa sexmaculata</i> (Pack.)	27 June-24 July	5
<i>Semiothisa signaria dispuncta</i> (Wlk.)	21 June-29 July	724
<i>Semiothisa pinistrobata</i> Fgn.	25 June-25 July	16
<i>Semiothisa orillata</i> (Wlk.)	25-28 June	3
<i>Iridopsis larvaria</i> (Gn.)	21 June-17 July	26
<i>Ectropis crepuscularia</i> (D. & S.)	27 June-29 July	23
<i>Protoboarmia porcelaria</i> (Gn.)	25 June-24 July	5
<i>Melanolophia canadaria</i> (Gn.)	21-26 June	6
<i>Eufidonia convergaria</i> (Wlk.)	25 June-20 July	12
<i>Biston betularia cognataria</i> (Gn.)	27 June-25 July	28
<i>Hypagyrtis piniata</i> (Pack.)	26 June-29 July	193 <sup>1</sup>
<i>Lomographa vestaliata</i> (Gn.)	21 June-15 July	30
<i>Cabera erythemaria</i> Gn.	21 June-25 July	41
<i>Cabera variolaria</i> Gn.	21 June-24 July	22
<i>Euchlaena obtusaria</i> (Hbn.)	17-18 July	2
<i>Euchlaena johnsonaria</i> (Fitch)	15-24 July	7
<i>Euchlaena marginaria</i> (Minot)	25 June	1
<i>Euchlaena tigrinaria</i> (Gn.)	4-18 July	2
<i>Euchlaena irraria</i> (B. & McD.)	2 July	4

## APPENDIX. Continued.

<i>Xanthotype urticaria</i> Swett	25 June-21 July	5
<i>Pero morrisonaria</i> (Hy. Edw.)	21 June-4 July	13
<i>Nacophora quernaria</i> (J. E. Smith)	26 June-18 July	4
<i>Campaea perlata</i> (Gn.)	21 June-25 July	12
<i>Tacparia atropunctata</i> (Pack.)	27 June	1
<i>Tacparia deterrenta</i> (Gn.)	21-26 June	8
<i>Homochlodes fritillaria</i> (Gn.)	21-29 June	5
<i>Metanema inatomaria</i> Gn.	21 June-29 July	11
<i>Metanema determinata</i> Wlk.	18-22 July	4
<i>Metarranthis amyrisaria</i> (Wlk.)	21-28 June	3
<i>Metarranthis hypocharia</i> (H.-S.)	25 June	1
<i>Anagoga occiduaria</i> (Wlk.)	21 June	1
<i>Probole amicaria</i> (H.-S.)	21 June-9 July	15
<i>Plagodis serinaria</i> H.-S.	27 June	3
<i>Plagodis phlogosaria</i> (Gn.)	26-29 June	7
<i>Plagodis alchoolaria</i> (Gn.)	21 June-4 July	4
<i>Caripeta divisata</i> Wlk.	25 June-29 July	78
<i>Caripeta piniata</i> (Pack.)	21 June-23 July	9
<i>Caripeta angustiorata</i> Wlk.	17-24 July	22
<i>Besma endropiaria</i> (G. & R.)	21-29 June	6
<i>Sicya macularia</i> (Harr.)	16-25 July	3
<i>Eusarca confusaria</i> Hbn.	16 July	1
<i>Tetracis cachexiata</i> Gn.	21 June-2 July	39
<i>Nematocampa resistaria</i> (H.-S.)	17-29 July	39
<i>Nemoria mimosaria</i> (Gn.)	14-15 July	2
<i>Cyclophora pendulinaria</i> (Gn.)	21 June-25 July	47
<i>Scopula cacuminaria</i> (Morr.)	18 July	1
<i>Scopula limboundata</i> (Haw.)	25 June-24 July	36
<i>Dysstroma citrata</i> (L.)	25-28 June	2
<i>Dysstroma walkerata</i> (Pears.)	21 June-14 July	4
<i>Dysstroma hersiliata</i> (Gn.)	15-29 July	3
<i>Eulithis explanata</i> (Wlk.)	16-29 July	55
<i>Ecliptopera silaceata albolineata</i> (Pack.)	21 June	1
<i>Hydriomena perfracta</i> Swett	21-25 June	2
<i>Hydriomena renunciata</i> (Wlk.)	21 June-29 July	79 <sup>2</sup>
<i>Hydria undulata</i> (L.)	14 July	2
<i>Rheumaptera hastata</i> (L.)	16 July	1
<i>Rheumaptera subhastata</i> (Nolcken)	26 June-8 July	2
<i>Mesoleuca ruficillata</i> (Gn.)	25 June	1
<i>Spargania magnoliata</i> Gn.	14 July	1
<i>Perizoma basaliata</i> (Wlk.)	25 July	1
<i>Xanthorhoe abrasaria congregata</i> (Wlk.)	25 June-13 July	8
<i>Xanthorhoe iduata</i> (Gn.)	12 July	1
<i>Xanthorhoe ferrugata</i> (Cl.)	21 June-4 July	3
<i>Xanthorhoe lacustrata</i> (Gn.)	16 July	1
<i>Hydrelia lucata</i> (Gn.)	26 June-18 July	11
<i>Hydrelia inornata</i> (Hulst)	25 June-17 July	9
<i>Eubaphe mendica</i> (Wlk.)	17-20 July	4
<i>Horisme intestinata</i> (Gn.)	29 June	1
<i>Lobophora nivigerata</i> Wlk.	26 June-29 July	63
<i>Lasiocampidae</i>		
<i>Malacosoma disstria</i> Hbn.	9-29 July	136
<i>Malacosoma americanum</i> (F.)	15-25 July	27

## APPENDIX. Continued.

## Saturniidae

<i>Dryocampa rubicunda</i> (F.)	21 June-21 July	31
<i>Anisota virginienensis</i> (Drury)	25 June	1
<i>Antheraea polyphemus</i> (Cram.)	21 June-22 July	8

## Sphingidae

<i>Ceratomia undulosa</i> (Wlk.)	21 June	2
<i>Sphinx gordius</i> Cram.	21 June-20 July	9
<i>Lapara bombycoides</i> Wlk.	21 June-24 July	18
<i>Smerinthus jamaicensis</i> (Drury)	21 June-25 July	14
<i>Smerinthus cerisyi</i> Kby.	21-29 June	2
<i>Paonias excaecatus</i> (J. E. Smith)	21 June-23 July	15
<i>Pachysphinx modesta</i> (Harr.)	21 June-23 July	43

## Notodontidae

<i>Clostera apicalis</i> (Wlk.)	21-26 June	2
<i>Nadata gibbosa</i> (J. E. Smith)	21 June-24 July	16
<i>Peridea basitriens</i> (Wlk.)	15-29 July	2
<i>Peridea angulosa</i> (J. E. Smith)	24-25 July	2
<i>Peridea ferruginea</i> (Pack.)	26 June-25 July	150
<i>Pheosia rimosa</i> Pack.	27 June-29 July	8
<i>Odontostia elegans</i> (Stkr.)	17-25 July	2
<i>Notodonta simplaria</i> Graef	15-24 July	7
<i>Gluphisia septentrionis</i> Wlk.	25 June-25 July	54
<i>Furcula cinerea</i> (Wlk.)	29 June-24 July	5
<i>Furcula modesta</i> (Hudson)	16-25 July	11
<i>Symmerista leucitys</i> Franc.	21 June	2
<i>Macrurocampa marthesia</i> (Cram.)	15-25 July	3
<i>Heterocampa umbrata</i> Wlk.	25 June-4 July	11
<i>Heterocampa guttivitta</i> (Wlk.)	29 June	1
<i>Heterocampa biundata</i> Wlk.	21 June-20 July	24
<i>Lochmaeus manteo</i> Doubleday	20-25 July	3
<i>Schizura ipomoeae</i> Doubleday	21 June-24 July	29
<i>Schizura badia</i> (Pack.)	21-27 June	2
<i>Schizura unicornis</i> (J. E. Smith)	15-24 July	10
<i>Schizura leptinoides</i> (Grt.)	25 June-23 July	8
<i>Oligocentria semirufescens</i> (Wlk.)	18-24 July	3
<i>Oligocentria lignicolor</i> (Wlk.)	26 June-29 July	89

## Arctiidae

<i>Eilema bicolor</i> (Grt.)	12-25 July	22
<i>Hypoprepia fucosa</i> Hbn.	4-29 July	54
<i>Haploa lecontei</i> (Guer.-Meneville)	9 July	1
<i>Holomelina laeta</i> (Guer.-Meneville)	29 June-25 July	31
<i>Holomelina aurantiaca</i> (Hbn.)	20 July	1
<i>Holomelina ferruginosa</i> (Wlk.)	11-22 July	7
<i>Pyrharctia isabella</i> (J. E. Smith)	14 July	1
<i>Spilosoma congrua</i> Wlk.	21 June-5 July	40
<i>Spilosoma virginica</i> (F.)	21 June-20 July	39
<i>Hyphantria cunea</i> (Drury)	21 June-24 July	182
<i>Platarctia parthenos</i> (Harr.)	27 June-17 July	3
<i>Apantesis virguncula</i> (W. Kby.)	27 June-20 July	5
<i>Halysidota tessellaris</i> (J. E. Smith)	13-19 July	2
<i>Lophocampa maculata</i> Harr.	21-29 June	48

## APPENDIX. Continued.

<i>Cynia tenera</i> Hbn.	26 June	1
<i>Ctenucha virginica</i> (Esp.)	10-19 July	4
Lymantriidae		
<i>Dasychira plagiata</i> (Wlk.)	26 June-25 July	69
<i>Leucoma salicis</i> (L.)	4-19 July	7
Noctuidae		
<i>Idia americanis</i> (Gn.)	21 June-29 July	50
<i>Idia aemula</i> Hbn.	14-20 July	11
<i>Idia rotundalis</i> (Wlk.)	21 July	1
<i>Zanclognatha pedipilalis</i> (Gn.)	18-24 July	3
<i>Zanclognatha protumnusalis</i> (Wlk.)	12-22 July	7
<i>Zanclognatha cruralis</i> (Gn.)	21 June-29 July	3
<i>Palthis angulalis</i> (Hbn.)	8-29 July	2
<i>Bomolocha baltimoralis</i> (Gn.)	26 June-20 July	11
<i>Lomanaltes eductalis</i> (Wlk.)	25 June	1
<i>Spargaloma sexpunctata</i> Grt.	21 June-21 July	6
<i>Pangrapta decoralis</i> Hbn.	21 June-20 July	26
<i>Parallelia bistriaris</i> Hbn.	21 June-29 July	5
<i>Catocala sordida</i> Grt.	24-25 July	3
<i>Chrysanympa formosa</i> (Grt.)	9-12 July	12
<i>Autographa precatationis</i> (Gn.)	29 June	1
<i>Autographa mappa</i> (G. & R.)	26 June	1
<i>Syngrapha altera</i> (Ottol.)	26 June-21 July	4
<i>Syngrapha octoscripta</i> (Grt.)	14 July	1
<i>Syngrapha epigaea</i> (Grt.)	15-21 July	2
<i>Syngrapha viridisigma</i> (Grt.)	18-24 July	2
<i>Syngrapha alias</i> (Ottol.)	21 June-20 July	22 <sup>3</sup>
<i>Syngrapha cryptica</i> Eichlin & Cunningham	24 July	1
<i>Syngrapha rectangula</i> (W. Kby.)	6-25 July	27
<i>Syngrapha microgamma nearctica</i> Fgn.	21 June	1
<i>Plusia venusta</i> Wlk.	17-19 July	2
<i>Baileya ophthalmica</i> (Gn.)	21 June	1
<i>Lithacodia muscosula</i> (Gn.)	21 June-10 July	4
<i>Lithacodia synochitis</i> (G. & R.)	8 July	1
<i>Lithacodia concinnimacula</i> (Gn.)	25 June-4 July	5
<i>Lithacodia carneola</i> (Gn.)	25 June-20 July	21
<i>Leuconycta diphteroides</i> (Gn.)	21 June-19 July	14
<i>Panthea acronyctoides</i> (Wlk.)	21 June-25 July	47
<i>Panthea pallescens</i> McD.	27 June-25 July	29
<i>Charadra deridens</i> (Gn.)	21 June-15 July	21
<i>Raphia frater</i> Grt.	21 June-29 July	152
<i>Acronicta americana</i> (Harr.)	21 June-24 July	18
<i>Acronicta dactylina</i> Grt.	14-25 July	9
<i>Acronicta lepusculina</i> Gn.	29 June-4 July	3
<i>Acronicta innotata</i> Gn.	21 June-25 July	19
<i>Acronicta tritona</i> (Hbn.)	15-19 July	3
<i>Acronicta grisea</i> Wlk.	21 June-24 July	18
<i>Acronicta superans</i> Gn.	15 July	1
<i>Acronicta hasta</i> Gn.	25 June	1
<i>Acronicta fragilis</i> (Gn.)	21 June-25 July	14
<i>Acronicta clarescens</i> Gn.	25 June-25 July	162
<i>Acronicta retardata</i> (Wlk.)	26 June-25 July	49

## APPENDIX. Continued.

<i>Acronicta impleta</i> Wlk.	29 June	1
<i>Acronicta noctivaga</i> Grt.	27-28 June	2
<i>Acronicta impressa</i> Wlk.	26 June	1
<i>Acronicta obliterata</i> (J. E. Smith)	26 June-14 July	4
<i>Agriopodes fallax</i> (H.-S.)	25 June-29 July	29
<i>Harrisimemna trisignata</i> (Wlk.)	15-29 July	4
<i>Apamea verbascoides</i> (Gn.)	23 July	1
<i>Agroperina cogitata</i> (Sm.)	10 July	1
<i>Amphipoea velata</i> (Wlk.)	23-25 July	3
<i>Euplexia benesimilis</i> McD.	21 June-25 July	36
<i>Phlogophora iris</i> Gn.	27 June-25 July	3
<i>Chytonix palliatricula</i> (Gn.)	21 June-25 July	78
<i>Dypterygia rozmani</i> Berio	25 June	1
<i>Hyppa xylinoides</i> (Gn.)	18-21 July	4
<i>Nedra ramosula</i> (Gn.)	24 July	1
<i>Callopietria mollissima</i> (Gn.)	25 June-25 July	43
<i>Callopietria cordata</i> (Ljungh)	21 June-29 July	162
<i>Proxenus miranda</i> (Grt.)	4 July	1
<i>Elaphria versicolor</i> (Grt.)	21 June-13 July	51
<i>Elaphria festivoides</i> (Gn.)	25 June-20 July	130
<i>Apharetra purpurea</i> McD.	15-29 July	24
<i>Oncocnemis riparia</i> Morr.	14 July	1
<i>Polia nimbosea</i> (Gn.)	24-25 July	4
<i>Polia imbriferia</i> (Gn.)	13-25 July	6
<i>Polia purpurissata</i> (Grt.)	24-25 July	3
<i>Polia detracta</i> (Wlk.)	4-20 July	8
<i>Polia goodelli</i> (Grt.)	16 July	1
<i>Polia latex</i> (Gn.)	21 June-10 July	18
<i>Melanchra adjuncta</i> (Gn.)	21 June-24 July	25
<i>Melanchra assimilis</i> (Morr.)	26 June-25 July	12
<i>Lacanobia subjuncta</i> (G. & R.)	24 July	1
<i>Lacanobia grandis</i> (Gn.)	21-28 June	14
<i>Lacanobia lutra</i> (Gn.)	21 June-25 July	89
<i>Lacanobia rugosa</i> (Morr.)	27 June-16 July	2
<i>Lacanobia legitima</i> (Grt.)	29 June-25 July	10
<i>Papestra biren</i> (Goeze)	27 June	1
<i>Lacinipolia lustralis</i> (Grt.)	27 June-24 July	17
<i>Lacinipolia anguina</i> (Grt.)	27 June	1
<i>Lacinipolia renigera</i> (Steph.)	29 July	1
<i>Lacinipolia lorea</i> (Gn.)	26 June-18 July	7
<i>Lacinipolia olivacea</i> (Morr.)	29 July	1
<i>Leucania multilinea</i> Wlk.	9-25 July	8
<i>Leucania insueta</i> Gn.	26 June-21 July	24
<i>Leucania inermis</i> (Fbs.)	9-16 July	4
<i>Leucania pseudargyria</i> Gn.	4 July	1
<i>Homorthodes furfurata</i> (Grt.)	2-24 July	77
<i>Orthodes crenulata</i> (Butler)	25 June-25 July	18
<i>Orthodes cynica</i> Gn.	21 June-29 July	268
<i>Euxoa divergens</i> (Wlk.)	5-19 July	2
<i>Ochropleura plecta</i> (L.)	21 June-25 July	29
<i>Diarsia jucunda</i> (Wlk.)	13-29 July	23
<i>Eurois astricta</i> Morr.	24-29 July	5
<i>Xestia dolosa</i> Franc.	15-29 July	10 <sup>4</sup>
<i>Xestia oblata</i> (Morr.)	8-20 July	3

## APPENDIX. Continued.

<i>Anomogyna elimata</i> (Gn.)	25-29 July	2
<i>Anomogyna badicollis</i> (Grt.)	24-29 July	5
<i>Anomogyna youngii</i> (Sm.)	15 July	1
<i>Aplectoides condita</i> (Gn.)	21 June-4 July	25
<i>Anaplectoides prasina</i> (D. & S.)	8-29 July	8
<i>Anaplectoides pressus</i> (Grt.)	15-25 July	4
<i>Eueretagrotis perattenta</i> (Grt.)	17-25 July	5
<i>Eueretagrotis attenta</i> (Grt.)	8-29 July	60
<i>Heptagrotis phyllophora</i> (Grt.)	27 June-25 July	39
<i>Cryptocala acadiensis</i> (Bethune)	22-24 July	4
<i>Noctua pronuba</i> L.	23-25 July	3

<sup>1</sup> Identification uncertain, may include or consist entirely of *Hypagyrtis unipunctata* (Haworth) (Geometridae).

<sup>2</sup> Includes *Hydriomena divisaria* (Walker) (Geometridae).

<sup>3</sup> Includes *Syngrapha abstrusa* Eichlin & Cunningham (Noctuidae).

<sup>4</sup> Identification uncertain, may include or consist entirely of *Xestia adela* Franclemont (Noctuidae).

A REVIEW OF THE *PHLOXIPHAGA* GROUP OF THE  
GENUS *HELIOTHIS* (NOCTUIDAE: HELIOTHENTINAE\*)  
WITH DESCRIPTION OF A NEW SPECIES

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**ABSTRACT.** The name *Heliothis phloxiphaga* at present embraces three distinct species: *H. phloxiphaga* G. & R., which is distributed throughout temperate North America, *H. acesias* F. & R., which occurs from Nevada and Idaho eastward to Ontario, and *H. australis*, new species, which is distributed from southern Mexico northward to New Mexico and Arizona.

**Additional key words:** taxonomy, cryptic species, *Heliothis acesias*, *Heliothis australis*, genitalia.

For several decades, *Heliothis acesias* F. & R. has been considered only a color form of *Heliothis phloxiphaga*. Although the valvae of the male genitalia show no evident differences, the everted vesica of the penis of the male and the bursa copulatrix of the female do show consistent differences. A third member of the group, a predominantly Mexican species, is larger than either *H. phloxiphaga* or *H. acesias* and also differs from these in the conformation of the basal portion of the vesica and of the bursa copulatrix.

*Heliothis phloxiphaga* G. & R.

Figs. 1, 4, 5, 8

*Heliothis phloxiphaga* Grote & Robinson (1867:187).

*Heliothis interjacens* Grote (1880:30).

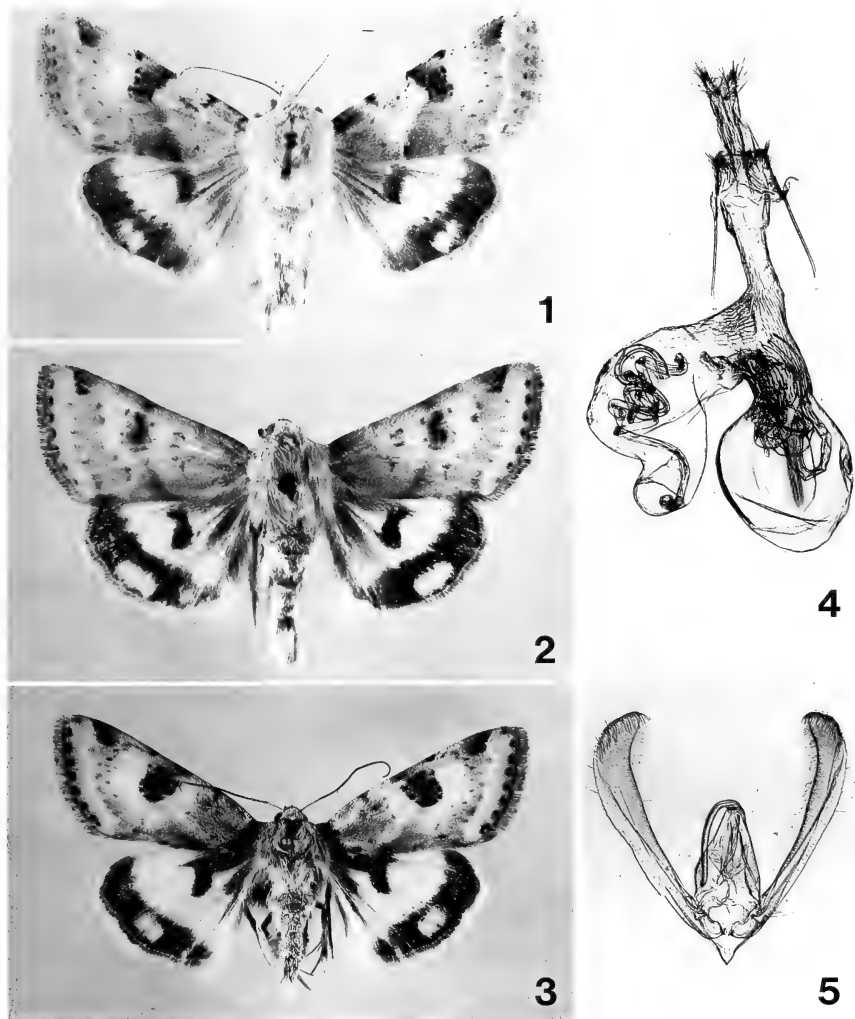
*Heliothis phloxiphaga* is one of North America's most common heliothentines; it is distributed throughout the United States and southern Canada and feeds on the flower and seeds of a wide variety of plants. The species is in flight throughout the summer months.

The forewing is light brown without a strong yellow suffusion. The median shade of the forewing (Fig. 1) angles outward from the trailing margin to the reniform spot, then is abruptly angled inward before continuing to the costal margin. The central area of the hindwing of

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\* Steyskal (1971) clearly demonstrated that Heliothentinae is the correctly derived name for the group. According to Opinion 1312 of the International Commission on Zoological Nomenclature, however, the name Heliothinae is to be made a conservandum as a subfamily name. This Opinion is without validity. When the submission was made by I. B. Nye in 1980, with a supporting addendum by the then-Secretary, R. V. Melville, I submitted a defense of the term Heliothentinae. My comments were suppressed by the Secretary and never submitted to the Commissioners. In view of this cavalier action, I requested of his successor as Secretary, P. K. Tubbs, that the matter be reopened. He refused. In his supporting addendum to Nye's submission, Melville noted that a noctuid moth, being nocturnal, "would be most unlikely to be exposed to the sun," and that Ochsenheimer's name was due to a printing error. This, of course, is completely fallacious. Obviously, Ochsenheimer was quite aware that the components of his proposed genus were often diurnally active.





FIGS. 1-5. Adults and genitalia of *Heliothis* spp. 1, *Heliothis phloxiphaga* G. & R., Aweme, Manitoba; 2, *H. acesias* F. & R., Spanish Fork, Utah; 3, *H. australis* n. sp., paratype, Lomas de Chapultepec, D.F., Mexico; 4, Female genitalia of *H. phloxiphaga*; 5, Valves of male genitalia of *H. phloxiphaga*.

the species is white. In the male genitalia (Figs. 5, 8), there are two elongate basal diverticula on the vesica, the one on the right noticeably stouter than the one on the left. In the female genitalia, the appendix bursae is slightly shorter than the fundus bursae (Fig. 4), and terminates in a short, slender, curving tail.

Expanse (Mean  $\pm$  SD):  $34.3 \pm 1.57$  mm ( $n = 30$ ).

*Heliothis acesias* F. & R.

Figs. 2, 6, 9

*Heliothis acesias* Felder & Rogenhofer (1872:pl. 108, fig. 42).*Heliothis luteitinctus* Grote (1875:426).

The known distribution of *Heliothis acesias* extends from north-eastern Nevada and southern Idaho, northward to southern Alberta, thence eastward to southern and eastern Ontario. It has been collected on dates between the middle of June and the end of September.

The species is of comparable size to *H. phloxiphaga*, but has yellowish-fawn forewings that are usually somewhat broader for their length than those of *H. phloxiphaga*. The median shade of the forewing (Fig. 2) is broadly excurved between the trailing and costal margins of the wing. The emarginating dots around the reniform and orbicular spots are usually more prominent than those of *H. phloxiphaga*. The central area of the hindwing is usually light yellow, less commonly white. In the male genitalia (Fig. 9), the base of the vesica is provided with only two shallow eversions. In the female, the appendix bursae (Fig. 6) is long and recurves anteriorly around the distal end of the fundus bursae.

Expanse:  $33.0 \pm 1.88$  mm ( $n = 24$ ).

*Heliothis australis* Hardwick, new species

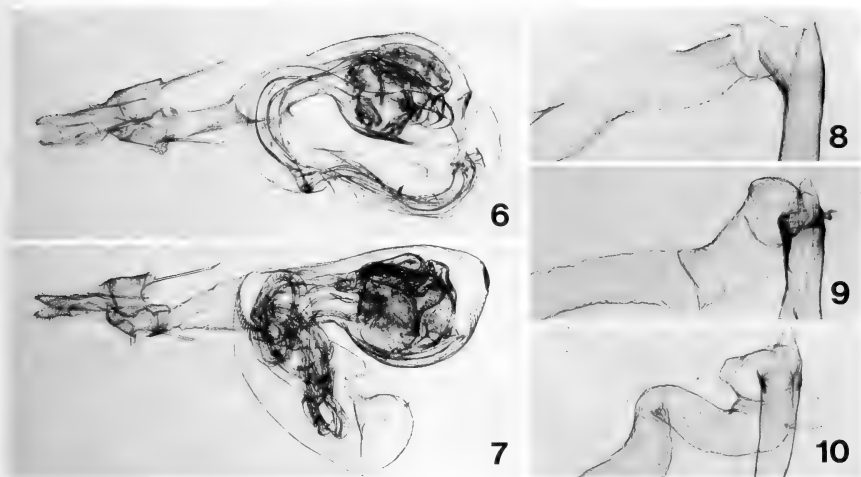
Figs. 3, 7, 10

Species usually larger than either *H. phloxiphaga* or *H. acesias*. Male with vestiture of head and thorax varying from reddish brown to olive-brown. Forewing light reddish brown, paler centrally than peripherally, with a very large and prominent reniform spot (Fig. 3). Median shade rather acutely excurved but not usually conspicuous. Central area of hind wing medium to dark yellow. In male genitalia, base of vesica (Fig. 10) provided with two stout diverticula, the left noticeably longer than right.

Female with maculation and coloring as in the male. Female genitalia (Fig. 7) with appendix bursae approximating fundus bursae in length.

Expanse:  $37.2 \pm 2.46$  mm ( $n = 17$ ).

**Type material.** Holotype, male: San Cristobal de las Casas, 7200 ft., Chiapas, Mexico, 5 May 1969 (J. E. H. Martin). Paratypes, 20 males, 6 females: Lomas de Chapultepec, D.F., Mexico, 9 May 1939, male; 10 June 1940, male; 18 June 1935, male; 28 June 1935 (2 males); 16 August 1976, male (T. Escalante). San Jacinto, D.F., Mexico, 24 July 1932, female; 19 October 1932, male; 2 October 1935, male. 24 mi. E El Salto, 7500 ft., Durango, Mexico, 15 & 17 July 1964, 2 males (J. E. H. Martin). Mexico, Mexico, 2 females. Bent, New Mexico, male, female. 13 mi. SE Cloudcroft, 7100 ft., New Mexico, 9 September 1975,



FIGS. 6-10. Genitalia of *Heliothis* spp. 6, Female of *H. acesias*; 7, Female of *H. australis*; 8, Apex of aedeagus and base of vesica of *H. phloxiphaga*; 9, Aedeagus and vesica of *H. acesias*; 10, Aedeagus and vesica of *H. australis*.

male, female (Lafontaine & Bowen). Cedar Crest, Sandia Mts., Bernalillo County, New Mexico, 4 July 1993, male (R. H. Leuschner). Prescott, Arizona, female. Alpine, White Mts., Apache County, Arizona, 24-25 July 1965, 2 males (R. H. Leuschner). Greer, 8300 ft., White Mts., Apache County, Arizona, 4 August 1969, 2 males (R. H. Leuschner). Springerville, Apache County, Arizona, 18-24 July 1971, male. Two males without data.

Holotype in the Canadian National Collection. Paratypes in the C.N.C., the U.S. National Museum, the Los Angeles County Museum, and the collection of R. H. Leuschner.

*Heliothis australis* is distributed from the state of Chiapas in southern Mexico northward to southern New Mexico and Arizona. The species has been collected on dates between early May and mid-October.

#### ACKNOWLEDGMENTS

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## LIFE HISTORY OF *PACHLIOPTA RHODIFER* (PAPILIONIDAE: TROIDINI)

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**ABSTRACT.** The Andaman clubtail, *Pachliopta rhodifer* (Butler), is one of three papilionids endemic to the Andaman and Nicobar islands, India. This elegant red-bodied swallowtail, with its unique red spatulate tail, previously was known only from the imago. We detail the life history of this species and discuss implications for butterfly conservation in these islands.

**Additional key words:** Aristolochiaceae, butterfly conservation, Andaman Islands, Nicobar Islands, India.

The Andaman and Nicobar islands have been identified as one of the provinces of the Indomalayan biogeographic realm requiring urgent attention to ensure adequate protection of their distinctive biological communities (Anonymous 1985, ICBP 1992). These islands are situated in the Bay of Bengal, Indian Ocean, between 6-14°N latitude and 92-94°E longitude, and consist of 306 islands. They stretch over 700 km and occupy a total area of 8249 km<sup>2</sup> (Anonymous 1986). The Andamans are separated from the Nicobars by the Ten Degree Channel, a distance of about 100 km. The two island groups have characteristic biotic elements, with each island group harboring a set of unique endemics (Anonymous 1986, Rao 1986).

On the basis of the number of endemics found in a region, Collins and Morris (1985) rate the Andaman and Nicobar islands sixteenth out of a total of 51 critical swallowtail faunas worldwide. In spite of the high priority ranking, no attempt has been made to study the life histories, food plants, and other requirements of *Graphium epaminondas* (Oberthür), *Papilio mayo* Atkinson, or *Pachliopta rhodifer* (Butler), the three endemic papilionids that are thought to be confined to Great Andaman (which includes the three neighboring islands of North, Middle, and South Andaman). Even Ferrar, who collected Lepidoptera on these islands for eight years, confined himself to the study of adults (Ferrar 1948).

Four species of *Pachliopta* are known to occur in the Andaman and Nicobar islands. Two of these, *P. coon* (Fabricius) and *P. hector* (Linnaeus), are protected by Indian law (Schedule I of the Indian Wildlife Protection Act, 1972, which came into effect on 2 October 1980). The former species is very rare and found only in the Nicobars in India; the latter is rare and confined to the Andamans and mainland India. Neither of the other two species, *P. rhodifer* and *P. aristolochiae* (F.), are considered threatened, even though the status of the endemic *P.*

*rhodifer* is not clearly known (Collins & Morris 1985). *Pachliopta rhodifer* is one of 17 species of the genus listed by Collins and Morris (1985) as requiring further monitoring and research.

We present below the results of our study on the life history of *P. rhodifer*, the only troidine swallowtail endemic to the Andaman Islands.

### Previous Collections

Ferrar (1948) states that there is a "good series" of *P. rhodifer* at the British Museum (Natural History) and at Calcutta. However, this species has proved to be elusive to those who have collected recently on these islands (Arora & Nandi 1980). Of nine expeditions from the Zoological Survey of India, Calcutta, only four succeeded in collecting this species. Cumulatively these surveys covered eight months of the year. They collected *P. rhodifer* during four months, i.e., January, March, April, and December. They collected a total of 16 males and four females. Nakamotu also succeeded in collecting four males and five females in the months of October and November 1979 (Tsukada & Nishiyama 1982).

*Pachliopta rhodifer* was known only from various places in South, Middle, and North Andamans (Ferrar 1948, Tsukada & Nishiyama 1982) until Arora and Nandi (1980) collected a male from Car Nicobar in December 1972. This male was perhaps a straggler and may have been blown over from S. Andaman to C. Nicobar (150 km). The food plant is found in the Nicobar Islands (Rao 1986), hence the butterfly could survive and breed there.

It is perhaps the scarcity of *P. rhodifer* in collections around the world that has resulted in its relatively high value in the insect trade (Smart & Smart 1982). One male specimen reportedly collected from North Andaman was listed for sale for \$400 U.S. We believe that rarity in collections is more a result of the stringent regulations imposed by the Government of India rather than a reflection of the rarity of the butterfly.

### MATERIALS AND METHODS

We discovered a last instar larva of *P. rhodifer* during a collecting trip to the forests of South Andaman in late October 1990. The discovery of the host of *P. rhodifer* was the key to searching for the early stages. Over a two-year period we visually searched mainly three localities for early stages: Garacharma, Mt. Harriet, and Chidiyatapu, all on the island of S. Andaman.

Upon locating host plants, which have a tendency to grow in patches, a thorough examination for eggs, larvae, and pupae was conducted. All

early stages discovered in the field were brought into the laboratory and housed in transparent, plastic jars of variable dimensions—the first and second instars in the smallest (6.5 cm high  $\times$  5 cm diameter), the third to fifth instars in medium (10 cm high  $\times$  7 cm diameter), and the final instar in the largest (19 cm high  $\times$  11 cm diameter) containers. Food (detached, whole, tender leaves) was supplied fresh every day. The rearing containers also were cleaned daily of all fecal matter and old food. Moisture that settled on the walls of the containers was wiped away with a dry cloth. A dry twig, slightly less than the height of the container, was placed diagonally in containers with final instars to facilitate pupation. All rearings were carried out in the laboratory at ambient temperature (23–30°C) and humidity (79%). Adults were released back into their habitat.

The study was conducted primarily on the main campus of the Central Agricultural Research Institute at Garacharma, approximately 6 km southwest of Port Blair on the island of S. Andaman, India. Patches of forest that have been retained in parts of the campus were found to support populations of the butterfly. Although subject to intense human intrusion, these patches continue to retain a number of plant and animal species that were a part of the original forest that once covered this area (Fig. 1). The larval food plant of *P. rhodifer* was found in a number of patches, some of which suffered more human damage than others. A large population of the immature stages was present in a relatively disturbed area where the larval food plant grew in the shrub layer close to the ground beneath the canopies of coconut, oil palm, and other trees. This area was subject to periodic weeding operations.

Additional observations were made during periodic visits to Chidiyatapu and Mt. Harriet, both situated in the southern half of S. Andaman. Although subject to less anthropogenic activities than the Garacharma site, these sites yielded fewer eggs and larvae of *P. rhodifer*, despite the fact that patches of the larval food plant at both these sites were more dense and healthier in appearance.

## RESULTS

*Thottea tomentosa* (Blume) Ding Hou (Aristolochiaceae), a low, woody, creeping under-shrub in the forests, was found to be the sole food plant of *P. rhodifer* (Figs. 1 & 2). The maximum height of the plant was 51.0 cm. Only the younger, densely tomentose terminal leaves were eaten; the lower older leaves were never fed upon. The older leaves were tougher and had a lower percentage of water than the younger leaves. After consuming most or all of the young, tender leaves of a plant, the larvae leave to find a new host plant.

We observed adults feeding on the flowers of *Vitex trifolia* L. (Ver-

benaceae), *Acacia* sp. (Mimosaceae), *Ixora* sp. (Rubiaceae) and *Intsia bijuga* (Coleb.) O.K. (Caesalpineaceae).

**Egg** (Fig. 3): Similar to other troidine eggs; pale orange with a smooth circular area on top.

**First instar:** Pale orange, partly suffused with black. Head, prothoracic shield, and anal legs deep glossy black; osmeterium pale orange. Tops of tubercles capped with about a dozen long, black setae. [This is characteristic of the early instars and unlike that of later instars.] Entire surface of body covered with minute hairs. Head capsule black in all instars.

**Second instar:** All larvae with similar color pattern from this instar on. The only difference between this and the following instars is that the red bands are incomplete along the mid-dorsal line, resulting in a continuous black mid-dorsal line, obliterated in the latter instars.

**Third through sixth instars** (Figs. 4 & 5): Rich purple-black, studded with intense orange-red and a few purple-black tubercles, interspersed with narrow bright orange-red bands running along the posterior margins of abdominal segments IV and VII. Head glossy black with a number of stiff bristlelike black setae. Clypeus dirty white and translucent.

On either side of the mid-dorsal line a row of bright-red tubercles on all segments except abdominal segments II, III, V, and VI, which are intense purple-black. A sub-dorsal row of orange-red tubercles on thoracic segments only, this row absent on the abdominal segments. A subspiracular row of tubercles on all thoracic and abdominal segments, orange-red except on abdominal segments V and VI where they are black. A complete row of sub-ventral tubercles, all bright orange-red except that on the last abdominal segment which is claret. A single small ventral tubercle exclusive to the second abdominal segment. All tubercles covered with setae, black on the red tubercles, silver-grey on the black tubercles. Ventral surface black, suffused with claret.

Spiracles black, outlined in white. Spiracles on abdominal segment IV in the black area apposite, but posterior to, the orange-red band. Spiracles on abdominal segments I and II progressively dorsal than those on all other abdominal segments, which form a straight line. Consequently, the subspiracular tubercles also have the I abdominal one highest, followed a little lower by the II abdominal tubercle; the remaining tubercles occur in a similar position on each segment, forming a straight line. Distances between the subspiracular and sub-ventral tubercles are variable in the anterior segments; the prothoracic and all abdominal tubercles of the two rows very close, their bases almost touching; the two spiracles on the meso- and metathoracic segments relatively further apart. The only tubercles on the prothorax are the subspiracular and the sub-ventral, which are deep orange-red. Dorsal space between the subspiracular tubercles covered by a light, orange-red smooth pad, faintly grooved along its mid-dorsal line. Black prothoracic shield behind this pad. A short red lateral band posteriorly, on the III abdominal segment starting from the base of the subspiracular tubercle and extending up to about  $\frac{2}{3}$  the distance to the dorsal tubercle. Red band on the IV abdominal segment posteriorly notched on the mid-dorsal line. Red band on abdominal segment VII divided mid-dorsally by a rich purple-black band. Depressed black spot in red bands of abdominal segments IV (above the base of the subspiracular tubercle) and VII (antero-dorsally at base of the subspiracular tubercle).

**Pupa** (Fig. 6): Orange-brown, resembling a dry leaf. Girdle black; cream lateral markings anterior to girdle. Two red, glistening, triangular areas on either side of the mid-dorsal line on anterior end of dorsal area of thorax. Blunt, dorsal horn with faint dorsal red line and foliaceous extensions/carinae from antero-ventral region, extending laterally to abdominal segment I. Circular, red spot in mid-dorsal region of abdominal segment II. Two orange-red areas or irregular spots on abdominal segment III laterally. Sparse, minute hairs in pits on pupal surface, increasing in number around dorsal end of spiracles. Additional pair of processes on either side of dorsal horn and on lateral margins of abdominal segment I.





FIGS. 1-7. Habitat and early stages of *Pachliopta rhodifer*. 1, Habitat of *P. rhodifer*; 2, *Thottea tomentosa*, the larval food plant, growing at the base of a tree; 3, Egg of *P. rhodifer*; 4, Third instar of *P. rhodifer*; 5, Fifth instar of *P. rhodifer*; 6, Pupa of *P. rhodifer*; 7, Adult male of *P. rhodifer*.

Eggs are laid singly. Females fly low over the undershrub layer, alighting on vegetation frequently, including the host plant, but do not often lay eggs. When laying an egg, the female alights on the host plant, bends her abdomen beneath the leaf surface, and lays an egg along or on one of the veins of a young leaf, but usually not on the midrib. Eggs generally are laid on the under surface of leaves of the

TABLE 1. Duration and size of the pre-imaginal stages of *P. rhodifer*.

	Eggs	I	II	III	IV	V	VI	PP	P
Duration (days)									
n	2	4	7	13	16	18	19	19	13
Range	>6	2-4	2-4	3-6	4-8	5-7	7-14	1-4	15-64
Mean	—	3	2.83	3.62	5.13	5.72	9.63	1.95	26.69
SE	—	0.41	0.26	0.25	0.24	0.16	0.39	0.14	5.19
Size (cm)									
n	—	2	6	13	16	18	20	—	19
Range	—	0.7-0.9	0.6-1.0	0.6-1.5	1.3-2.2	2.3-3.1	2.8-3.7	—	3.1-3.8
Mean	—	0.8	0.85	1.16	1.67	2.68	3.31	—	3.44
SE	—	0.1	0.06	0.07	0.06	0.06	0.07	—	0.04

\* Total life cycle: Mean from I instar to adult = 58.6 days = 59 days. Mean from egg to adult = over 64.6 days = over 65 days.

host plant or rarely on adjacent vegetation. Because the undersurfaces of *Thottea* leaves generally are encrusted with a layer of mud, the veins are the only places where eggs can be laid safely without being dislodged. Only one egg is laid on each leaf. On one occasion, one egg was found on a blade of grass; another was found on a cane leaf. The incubation period is at least six days, after which the first instar larvae emerge. Larvae eat the chorion and begin to feed on the tender young leaves (see Table 1 for sizes and durations of all stages).

The first instar larva appears to remain on the leaf on which it hatches; later instars move not only from one leaf to another on the same plant, but also from plant to plant. Later instars have been observed moving along the ground, probably in search of a new host plant; host plants tend to have clumped distributions. Larvae are forced to move from plant to plant because they feed exclusively on the new flush.

Although we were able to find all stages from eggs to last larval instar, we never discovered prepupae or pupae, suggesting that pupation occurs away from the host plant.

The prepupal period usually lasts about two days but in one case it lasted four days.

The total life cycle lasts about 65 days. As the eggs were collected from the field, and not from females bred in the laboratory, it was not possible to ascertain when they had been laid, leading to an uncertainty

TABLE 2. Duration and head capsule measurements of *P. rhodifer* larva when passing through seven instars ( $n = 1$ ).

	Egg	I	II	III	IV	V	VI	VII
Duration (days)	>3	3	4	4	5	5	7	10
Width of head capsule (mm)	—	0.9	1.2	1.7	2.3	2.9	3.9	—

TABLE 3. Mortality pattern in captive pre-imaginal stages of *P. rhodifer* in S. Andaman.

	Egg	I	II	III	IV	V	VI	PP	P
Total collected	5	4	7	13	16	19	21	23	23
No. dead	3	—	—	—	—	1	1	3	9
Percent mortality	60	—	—	—	—	5	5	13	39

in the incubation period and consequently in the number of days taken to complete the entire life cycle.

When we searched for the eggs and larvae of *P. rhodifer* in April, the driest month in the year, we could find only one egg of the butterfly and no new flush of the food plant. On hatching, the larva had to be fed older, poor quality leaves. This individual passed through seven larval stages. Nevertheless, the total larval period did not vary from those rearings that had six instars. Dimensions of the head capsules and the durations of larval instars of this individual are presented in Table 2.

Two eggs and a third instar larva collected in the field were parasitized. The egg parasitoid was identified as *Telenomus (Aholcus)* sp. (Scelionidae: Hymenoptera). The larval parasitoid could not be identified, as the hymenopteran adults failed to emerge from their cocoons. A certain degree of mortality (Table 3) also was noticed while rearing the butterfly. From the first to fourth instar, all larvae survived. Mortality occurred in the egg stage and in larval instars V and VI, as well as during the prepupal and pupal stages. Mortality was highest in the egg and pupal stages.

One instance of mating in flight was observed at about 1100 h in the Garacharma farm of the C.A.R.I. campus when a pair *in copula* flew at a height of about 5–6 meters and alighted on the branch of a tree well beyond our reach. A mating pair also was seen at about 1700 h on a blade of grass along an earthen embankment at the base of Mt. Harriet.

## DISCUSSION

Thirteen genera in the tribe Troidini feed on aristolochiaceous food plants during their larval stages (Igarashi 1984). Of the four species of *Pachliopta* found in the Andaman and Nicobar islands, two are rare and their local food plants remain unknown. The other two species, *P. aristolochiae* and *P. rhodifer* (Fig. 7), feed exclusively on *Thottea tomentosa*. *Thottea tomentosa*, though only locally abundant, is much more frequent in its occurrence than *Aristolochia tagala* Cham., the only other member of the Aristolochiaceae found on these islands (Ding

Hou 1981, Rao 1986). Although we found *P. rhodifer* and *P. aristolochiae* occurring together in our study sites, we did not find them in numbers large enough to suggest intra-specific competition during the larval stage. Therefore we feel that there are no specific larval adaptations that have arisen as a result of competitive interactions. It is interesting to note that although *Thottea* is widely distributed in the Malesian region and on the Indian Subcontinent (Ding Hou 1981), *P. rhodifer* has failed to expand its range. In fact, although *T. tomentosa* occurs in both the Andaman and Nicobar islands (Rao 1986, specimens at the Botanical Survey of India herbarium, Port Blair), *P. rhodifer* apparently is restricted to Great Andaman [with the exception of the single stray record of the species from Car Nicobar by Arora and Nandi (1980)].

Open water between islands may be an effective barrier preventing dispersal of this species. Though Tsukada and Nishiyama (1982) indicate that it is an exceedingly slow flyer, our observations reveal that the species is capable of fairly fast (though not vigorous), bobbing flight when disturbed.

The presence of six larval instars, instead of the usual five as in all other Papilionidae, lends credence to classifying *P. rhodifer* as a distinct species and not as a form of *P. coon* (Miller 1987). Although the larvae may pass through an additional instar when under stress (possibly because of food of inferior quality), six instars is the norm for *P. rhodifer*.

Like all troidines, *P. rhodifer* has red-tuberculate, *Aristolochia*-feeding larvae that are aposematically colored and probably unpalatable to predators (Hancock 1983, 1988, DeVries 1987). Because we found larvae during most months of the year, we suspect that it is multivoltine, as in other *Pachliopta* species (Igarashi 1984). *Pachliopta rhodifer* lays eggs singly and the larvae are solitary feeders, thus conforming to the pattern in other *Pachliopta* (Igarashi 1984).

Tsukada and Nishiyama (1982) state that adults of *P. rhodifer* 'become active only at dusk and fly toward 5 p. m.' Our studies failed to corroborate this observation. We observed *P. rhodifer* in flight in the morning and in the evening (from 0700 h to 1800 h).

In the Oriental region, only the peripheral areas such as the Andaman Islands are rich in endemic Papilionidae (Hancock 1983). Williams et al (1991) suggest the incorporation of the extent of geneological differences into the biodiversity measure in addition to the endemicity criterion. If this is done, the Andaman Islands are likely to move further up the priority list presented by Collins and Morris (1985) because the three endemic papilionids in the Andamans belong to three different tribes—Leptocircini, Papilionini, Troidini (Hancock 1983).

This diversity of endemics, together with the fact that all endemics

so far have been reported almost exclusively from Great Andaman, indicates that butterfly conservation in the region is extremely important. The Great Andaman, which makes up well over half the area of the Andaman Islands (constituting about 70 percent of the total land area of the Andamans) has been facing great pressure from human activities. Since the mid-1800's it has been increasingly cleared of its natural vegetation to meet the growing demands of a rapidly expanding human population that favors settlements close to Port Blair, the capital of these islands. The food plants of at least two endemic species of Papilionidae, *Graphium epaminondas* and *P. rhodifer*, both of which have patchy distributions in the forests of these islands, may be facing a threat from these activities of man. There is thus an urgent need for studies of the type being conducted by Pollard (1977) to assess the status of the endemic species of Lepidoptera, particularly when the clamor for the 'development' of these islands through increased urbanization and industrialization is on the rise.

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RECENT INTRODUCTIONS OF RIPARIAN NOCTUID  
MOTHS FROM THE PALAEARCTIC REGION TO  
NORTH AMERICA, WITH THE FIRST REPORT OF  
*APAMEA UNANIMIS* (HÜBNER)  
(NOCTUIDAE: AMPHIPYRINAE)

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**ABSTRACT.** The Palearctic moth *Apamea unanims* (Hübner) (Noctuidae: Amphipyridae) is reported as new to North America on the basis of a female specimen from the vicinity of Ottawa, Ontario, Canada, collected 11 June 1991. The larva of this species feeds on riparian grasses such as *Phragmites* and *Phalaris* (Poaceae). Two other recent introductions of Noctuidae from the Palearctic to North America, *Apamea ophiogramma* (Esper) and *Rhizedra lutos* (Hübner) (Amphipyridae), both apparently established in several areas, feed as larvae on these same plants. The apparent synchronous establishment of three Palearctic species with similar ecological associations suggests that they may have arrived by similar means, possibly aided by the modern shipping practices.

**Additional key words:** *Rhizedra lutos*, *Apamea ophiogramma*, *Phragmites*, *Phalaris*.

Among the 95 species of Noctuidae recently listed as Holarctic by Mikkola et al. (1991), 26 were considered as probable introductions by man or assisted by man. Thirteen are common European species, probably transported from Europe to the west (or over the Pacific). No corresponding introductions from North America to Europe are known. Possible reasons for this bias are introduced European plants providing host plants in North America, but not vice versa, and the possible saturation of European agroecosystems (Mikkola et al. 1991).

The two most recent introductions differ from earlier ones in that the species are associated with moist habitats (Mikkola et al. 1991). *Rhizedra lutos* (Hübner) (Figs. 6–8) was reported by McCabe and Schweitzer (1991) from New Jersey, and *Apamea ophiogramma* (Esper) (Figs. 4, 5) by Troubridge et al. (1992) from the Vancouver area, British Columbia. We list several new localities for both of these species from eastern North America.

We would like to draw the attention of North American lepidopterists to these two species and, in particular, to a third amphipyridine species first found in North America in 1991.

*Apamea unanimitis* (Hübner, 1813)

The first North American specimen was collected in Pinhey Forest Preserve, Nepean, 12 km SW of Ottawa on 11 June, 1991 (J. D. Lafontaine). This female specimen (Fig. 1) was caught at light in a garden at the margin of a mixed forest, in the garden there is a small artificial pond with tall grasses and sedges transported from nearby ditches.

*Apamea unanimitis* is a small *Apamea* with a wingspan (i.e., distance of forewing outer margins in a well spread specimen) of 29 to 33 mm (mean 30.9 mm♂♂, 31.7 mm♀♀; the difference is significant, Mikkola & Jalas 1979). It is a highly variable species, and the forewing coloration varies from pale luteous gray brown with a darker costal area to unicolorous blackish brown (cf. Figs. 1–3). The median area is weakly marked. The presence of fine white lining on the outer side of the reniform spot is a good specific character.

The species is not closely related to any North American *Apamea* species but is most likely to be misidentified as a dark form of *Apamea remissa indocilis* (Walker). It can be distinguished from *remissa* by its white-lined reniform spot. The most obvious feature distinctive from "*Oligia*" *fractilinea* (Grote), and from the Palaearctic *Mesapamea secalis* (Linnaeus), is the large hindwing discal spot (well visible on the underside of the wing).

The determination of male specimens of *A. unanimitis* may be easily confirmed by brushing the valva. The cucullus is upright as in most *Apameas*, and a large sclerotized, coiled digitus is present at the anterior lower corner.

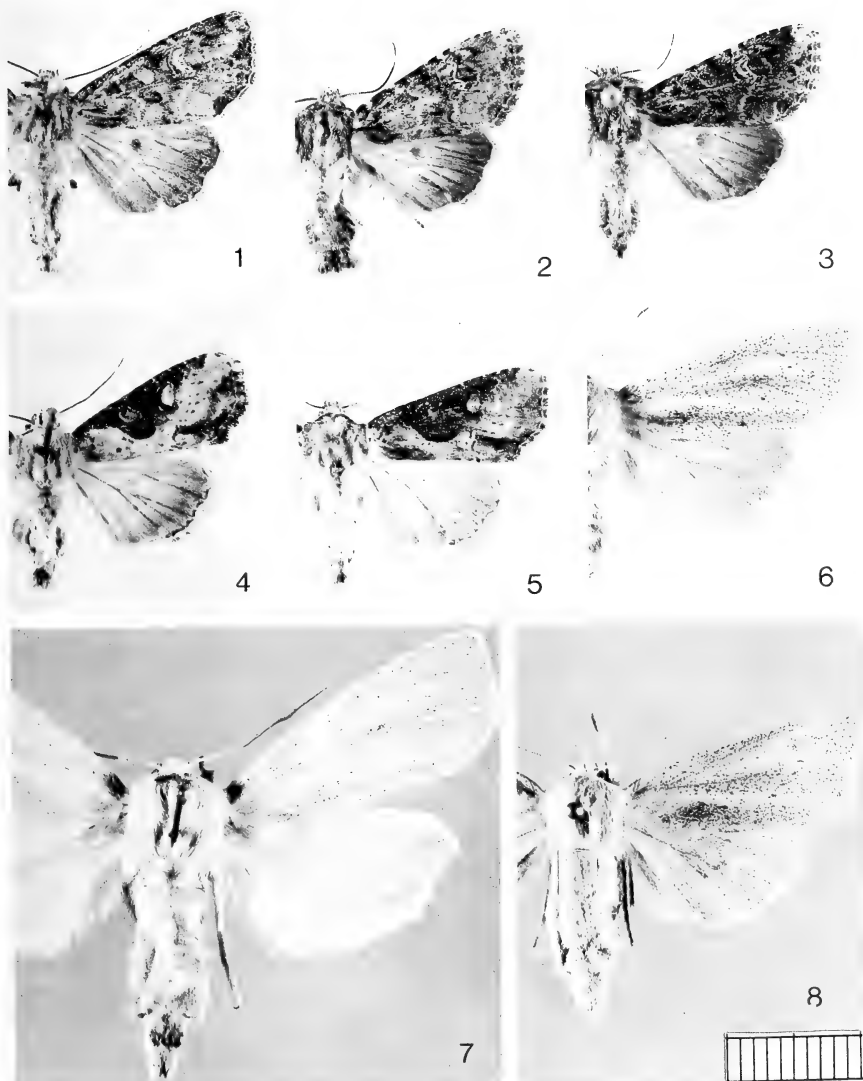
*Apamea unanimitis* occurs from the Pyrenees and northern Italy to the central parts of Fennoscandia (about the 63rd parallel) in Europe, and from there the distribution extends through Russia, Caucasus, and Siberia to the Amur River. The species is mainly rare and localized. However, in suitable habitats, such as rocky sea-shores, the species may be abundant in June and early July. It can be collected most easily by sugaring.

The larva feeds between the leaves of riparian grasses such as *Phragmites*, *Phalaris*, and *Glyceria* overwintering fully grown and pupating in the spring inside broken stems (Mikkola & Jalas 1979). The larva overwinters in grass tussocks, under loose bark, and in rotten wood, and pupates in the early spring in a compact cocoon in the soil (Bretherton et al. 1983).

*Apamea ophiogramma* (Esper, 1793)

*Apamea ophiogramma* was first reported from Langley, British Columbia; 4 specimens were collected at light in 1989, 19 in 1990 and 38 in 1991, between late June and late August, all of them of the typical





FIGS. 1-8. Specimens of *Apamea unanimitis* (Hübner), *A. ophiogramma* (Esper) and *Rhizedra lutosus* (Hübner) from North America and Europe. 1-3, *A. unanimitis*—1, female, Canada, Ontario, Ottawa 12 km SW, Pinhey Forest, 11 June 1991, leg. J. D. Lafontaine; 2, male, Finland, U: Porvoo, 8 June 1930, leg. E. Suomalainen; 3, female, Finland, U: Hanko, 18 June 1983, leg. Nupponen; 4-5, *A. ophiogramma*—4, female, Canada, B.C., 5 km E Langley, 24-30 June 1990, leg. J. Troubridge; 5, male form "maerens", U: Tvärminne, 9 August 1981, leg. A. Järvelä; 6-8, *R. lutosus*—6, male, Finland, U: Espoo, 16 September 1960, leg. P. Utrio; 7, female, U.S.A., N.J., Cumberland Co., Port Norris, salt marsh, 30 September 1988, leg. D. Schweitzer; 8, female, England, 6 September 1892, leg. T. Tunstall.

(pale) form (Troubridge et al. 1992). We know of the following specimens from eastern North America:

- Vermont, South Burlington, 28 July 1991, J. R. Graham, ♀ f. "*maerens*"
- New York, Albany Co., Pinebush, 1991, T. L. McCabe, 1 ex. f. "*maerens*"
- Quebec, St.-Jean de Martha, 26 July 1992, T. Thouin, ♂ f. "*typica*"
- New Brunswick, Edmundston, 7 August 1992, H. Hensel, ♂ f. "*maerens*".

*Apamea ophiogramma* is a small noctuid with a wingspan of 26 to 32.5 mm. It is easily recognized by the snake-like line between the blackish anterior and the pale brownish posterior part of the forewing. The forewing groundcolor is smoky gray in the melanic form "*maerens*" Staudinger, and the contrast of the "snake line" is correspondingly weaker (Fig. 5). The melanic form in Helsinki, Finland constitutes about 40 percent of the population (Mikkola & Jalas 1979), but this form is not mentioned from Japan (Sugi 1982). The male genitalia of the species were illustrated by Troubridge et al. (1992). Sugi (1982) moved the taxon to the genus *Oligia*, but we prefer to retain it in *Apamea* until a generic revision of the Apameini is completed.

The species is distributed from western Europe to Japan. The larva feeds on shore grasses, such as *Phragmites*, *Phalaris* and *Glyceria* (e.g., Mikkola & Jalas 1979), living within the stems, leaving them to overwinter in the soil, and returning to the stems in the spring. It pupates in the soil (Bretherton et al. 1983). The moths fly mainly from mid-July to mid-August, and they can be collected near shores and wetlands at light or by sugaring.

#### *Rhizedra lutosa* (Hübner, 1803)

This species was first reported in North America from the salt marshes of Delaware Bay, Cumberland County, New Jersey (McCabe & Schweitzer 1991) where 18 moths (5♂♂ 13♀♀) were collected in 1988 and 1989. The extreme dates were 30 September and 4 November. We now report two additional collections:

- New York, Albany Co., Pinebush, 1991, T. L. McCabe
- New York, Catskill, West Shokan, 1991, J. G. Franclemont.

This is a bulky fall-flying species that can be recognized easily from the straw-colored, apically sharp forewing. The groundcolor may have a reddish-brown hue. The wingspan varies in Finland from 34 to 52.5 mm, the females being on average larger than the males, and the forewing is "almost always characteristically irrorate with black scales"

(Mikkola & Jalas 1979). The specimen from New Jersey (Fig. 7) is uncharacteristically large and pale. The handbooks from Central Europe illustrate similar unicolorously pale moths (e.g., Bretherton et al. 1983). The male genitalia were illustrated by McCabe and Schweitzer (1991).

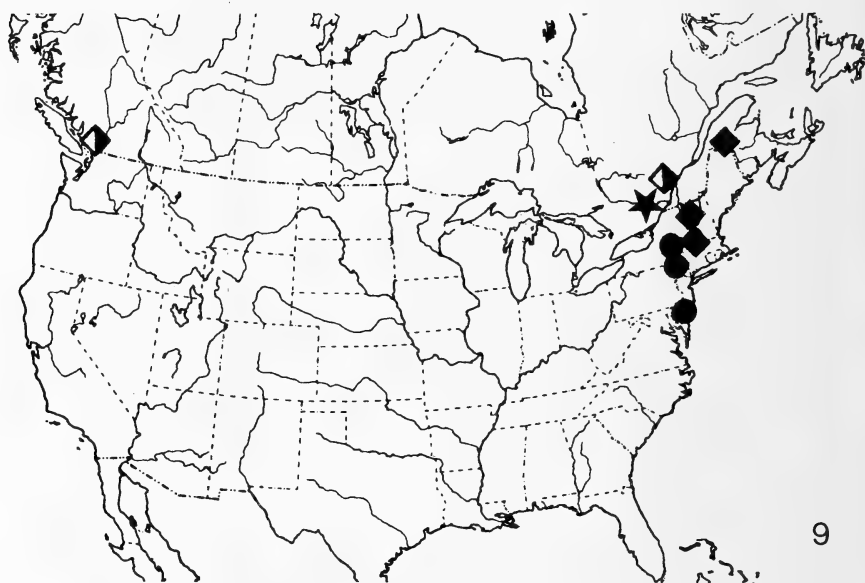
The species is distributed from western Europe to Tibet and Japan. In Europe, *R. lutosa* is thought to be monophagous on *Phragmites australis*. The larva lives inside the stem bases and rhizomes of reeds that grow on dry land, causing blanching of the leaves; it pupates in the reed-humus amongst the rhizomes; the egg overwinters (Mikkola & Jalas 1977, Bretherton et al. 1983). The moths fly mainly from late August to early October, in and near reeds but, as in many other noctuids of this habitat, the females may disperse far from suitable habitat. The moths are attracted to light but rarely come to sugar baits.

#### DISCUSSION

The Canadian record of *Apamea unanimitis* fits well with the European flight time because in Europe the species is one of the earliest *Apameas* to appear in late spring and early summer. The around 5 yards long garden pond hardly supports a permanent population of *A. unanimitis*, but the species could be established along the shores of Ottawa and Rideau rivers, the latter two miles away, where *Phragmites* grows. The other two introduced riparian species seem to be relatively widespread, but the sudden accumulation of new observations suggests that they are newcomers.

The external appearance of the moths, combined with geographical factors, permits some inferences about the possible sources of the founder individuals. The monomorphic population of *Apamea ophiogramma* in western North America evidently has been imported from the Far-East or Japan where the melanic form seems not to occur (there occur wild type females in eastern North America, too, but importation from there seems improbable). As expected, the eastern population might have originated in the industrialized areas of Western Europe (the founder could have been a single heterozygous female which would have produced both pale and melanic forms). The very pale appearance of the American specimens of *Rhizedra lutosa* points to an origin in Great Britain or in continental Central Europe.

It is curious that three species associated with riparian grasses should appear in North America in such a short period. It seems possible that modern shipping practices may have contributed to the spread of these species. Because one of the species may overwinter as a pupa within *Phragmites* stems or close to them, the other probably lays overwintering eggs on *Phragmites*, and the third spends the winter as a medium-



9

FIG. 9. Distribution of collecting localities of the three European Apameini moths in North America. ★ = *Apamea unanimitis*; ◐ = *Apamea ophiogramma*, half-filled = typical form, filled = melanic form; ● = *Rhizedra lutosa*.

sized larva associated with riparian grasses, it is possible that all three species have been transported with *Phragmites*, or with other riparian vegetation.

Soils are no longer used as ship ballast, but new shipping techniques may provide clues. Containers are kept in large storage yards in shore areas, and when they are transported into the ships, grass turfs may enter the ships. On the other hand, the reproductive strategy of *Phragmites* may enhance introduction. The plant mainly reproduces asexually from the rhizomes, and these often form dense mats along the shore. In the winter, the ice movements remove such mats, and rafts several meters in length can be seen on or near the shores. Pieces of them may enter ships through the open gates. Thus, container ships may transport reed material across the ocean, both from Europe to eastern North America, and from eastern Asia to the west coast of North America.

If the appearance of these three riparian species reflects a similar history of introduction, other Palaearctic riparian species could be expected to appear in North America, including the following species

feeding on *Phragmites* as larvae: *Archanara* spp., *Chilodes maritima* (Tauscher), *Arenostola phragmitidis* (Hübner), *Photedes brevilinea* (Fenn), *Mythimna pudorina* (Denis & Schifferrmüller), *M. straminea* (Treitschke), *M. obsoleta* (Hübner) and *Senta flammea* (Curtis). Species of other lepidopteran families living as larvae on *Phragmites* or on other riparian grasses also may be introduced.

#### ACKNOWLEDGMENTS

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SYSTEMATIC POSITION OF *SIBATANIOZEPHYRUS* AND  
DESCRIPTION OF A NEW SPECIES FROM TAIWAN  
(LYCAENIDAE: THECLINAE)

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**ABSTRACT.** The systematic position of the *Fagus*-feeding genus *Sibatanozephyrus* was examined using cladistic methodology. This formerly monotypic genus, confined to eastern Asia, previously was lumped with *Quercusia*, a monotypic genus confined to Europe. If the two genera are combined, they form a paraphyletic taxon in the preferred cladogram. Hence, this analysis provides support for maintaining the two as distinct genera. *Sibatanozephyrus kuafui*, new species, is described and illustrated from Taiwan. The discovery of the new species has interesting biogeographic interpretations.

**Additional key words:** *Quercusia*, *Fagus*-feeding, Theclini, China, Japan.

Members of *Sibatanozephyrus* are moderate sized (forewing length 15.0-18.6 mm) Theclini "hairstreak" butterflies that live exclusively in beech (*Fagus* spp.; Fagaceae) forests. Males spend the majority of their adult life flying high around the canopy of beech trees, showing their magnificent metallic blue colors. In contrast, females sit motionless most of the time, perched in the vegetation, with their somber brown wings folded. The larvae of *Sibatanozephyrus* feed exclusively on soft new foliage of the host, which is available only in early spring. As a result of the narrow availability of appropriate larval food, members of *Sibatanozephyrus* are univoltine.

The taxonomic status of *Sibatanozephyrus* has been the subject of considerable controversy. Prior to the discovery of the new species described below, the genus was considered monotypic, accommodating the single species *S. fujisanus* (Matsumura), which is restricted to Japan. On the basis of similarities in the female genitalia, *Sibatanozephyrus* was lumped by Shirôzu and Yamamoto (1956) with the monotypic genus *Quercusia*, which includes the single species *Q. quercus* (Linnaeus) restricted to Europe. Shirôzu and Yamamoto (1956) did not dismiss the possibility that the two may require different genera. Although the female genitalia of the two are similar, other characters (i.e., male genitalia and relative length of the discoidal cell of the forewing) are moderately divergent, suggesting that the two genera may not form a monophyletic lineage. This taxonomic difficulty has been manifested in nearly every treatment that included *Sibatanozeph-*

TABLE 1. Number of species of *Fagus*, *Sibataniozephyrus*, and Theclini represented in the world with special reference to Asia: EU, Europe; AC, mainland China; AT, Taiwan; AJ, Japan; NA, North America. (Data resources: D'Abrera 1993, Inomata 1986, Makino 1989, Shirôzu 1961, Walters, 1964, Zhang 1987.)

	<i>Fagus</i>	<i>Sibataniozephyrus</i>	Theclini
EU	2	0	3
AC	6	0	58+
AT	1	1	25
AJ	2	1	24
NA	1	0	3

*yrus* since that time (e.g., Kawazoé & Wakabayashi 1976, Saigusa 1983, Fukuda et al. 1984, D'Abrera 1993).

In 1986 Inomata (1986) proposed the genus *Sibataniozephyrus* for the species *fujisanus*, but provided no phylogenetic analyses to support this placement. Indeed, no taxonomic level within the Theclini has been the subject of cladistic analysis to elucidate the phylogeny.

*Sibataniozephyrus* represents the only *Fagus*-feeding member of Theclini. Because the distributional centers of both *Fagus* and Theclini are located in China (Table 1), where the *Fagus*-feeding behavior likely evolved, it seems unusual that *Sibataniozephyrus* was absent from there. Intrigued by this incongruity, we began extensive collecting in *Fagus* forests on Taiwan in 1986. These efforts finally produced an undescribed species of *Sibataniozephyrus* in 1992.

#### MATERIALS AND METHODS

A cladistic analysis of *Sibataniozephyrus* and its nearest relatives was conducted in an attempt to elucidate the relationship between *Quercusia* and *Sibataniozephyrus*. In addition to these two, the following genera were included in the cladistic analysis: *Chrysozephyrus* Shirôzu & Yamamoto, *Thermozephyrus* Inomata, *Neozephyrus* Sibatani & Ito, *Favonius* Sibatani & Ito (divided into two OTU's because it contains a remote member *F. saphirinus* Staudinger), and *Austrozephyrus* Howarth. Selection of these genera was based primarily upon studies by Shirôzu and Yamamoto (1956) and Eliot (1973). Two remote genera, *Japonica* Tutt and *Euaspa* Moore, were included in the analysis as outgroups. More than one outgroup was used because multiple outgroups will generate the most parsimonious cladogram globally (Madison et al. 1984). *Japonica* was selected because its members retain a large number of ancestral characters (Shirôzu & Yamamoto 1956). *Euaspa* was chosen because the systematic position of *Austrozephyrus* was suspected to have common rooting with this genus (Saigusa 1983).

Whenever possible, we used the type species of the above genera.

When insufficient material was available for the type species, we used specimens of closely related species in the same genus. For selection of appropriate species and characters for the analysis, we consulted the following literature: Shirôzu and Yamamoto (1956), Shirôzu (1960) and Shirôzu and Saigusa (1970). Together, these publications contain detailed illustrations of numerous species of the genera examined in the cladistic analysis. All of the species substituted for the type species shared the same character states with the type species for all of the characters used in the analysis. Terminology for genitalic structures used in the character analyses and descriptions follow Klots (1970).

**Material examined (type species of each genus in bold):**

*Chrysozephyrus disparatus* (Howarth) (1♂, Taiwan); *C. duma* (Hewitson) (1♂, Nepal); *C. kabrua* (Tytler) (2♂, Taiwan); *C. nishikaze* (Araki & Sibatani) (1♂, Taiwan); *C. rarasanus* (Matsumura) (6♂, Taiwan); *C. smaragdinus* (Bremer) (4♂1♀, Japan); *C. souleanus* (Riley) (2♂2♀, China); *C. yuchingkinus* Murayama & Shimonoya (2♂, Taiwan).

*Thermozephyrus ataxus* (Doubleday & Hewitson) (3♂3♀, Japan; 1♂1♀, Taiwan).

*Neozephyrus japonicus* (Murray) (3♂, Japan); *N. helenae* Howarth (1♀, China); *N. taiwanus* (Wileman) (3♂1♀, Taiwan).

*Sibataniozephyrus fujisanus* (Matsumura) (3♂8♀, Japan); *S. kuafui* Hsu & Lin (24♂1♀, Taiwan).

*Quercusia quercus* (Linnaeus) (2♂2♀, France; 2♂1♀, Belgium).

*Favonius jezoensis* (Matsumura) (6♂2♀, Japan); *F. latifaciatus* (Shirôzu) (2♂1♀, Japan); *F. orientalis* (Murray) (3♂, Japan); *F. saphirinus* (Staudinger) (4♂1♀, Japan); *F. taxa* (Bremer) (4♂, Japan).

*Austrozephyrus obsolon* (Hewitson) (2♂4♀, Malaya).

*Japonica lutea* (Hewitson) (1♂, Japan; 2♂5♀, Taiwan); *J. saepestriata* (Hewitson) (4♂8♀, Japan; 1♂1♀, China).

*Euaspa milionia* (Hewitson) (2♂, Taiwan; 1♀, Nepal).

The cladistic analysis was performed primarily using Hennig 86 version 1.5 with implicit enumeration option (Farris 1988). Hennig 86 does not allow multiple outgroup assignment, so only *Japonica* was assigned as outgroup, although *Euaspa* was retained in the analysis. *Euaspa* was expected to be linked with *Austrozephyrus* if they are more related to each other than to the rest of the ingroup members. PAUP version 2.4 also was employed to check the results, using global branching swapping and multiple parsimony options (Swofford 1985). PAUP allows multiple assignments of outgroups, so both *Japonica* and *Euaspa* were regarded as outgroups in that analysis.

**Characters Used to Construct Hypothetical Phylogeny  
for *Sibataniozephyrus* and Its Related Genera**

Because of the uniform external features among these genera, genitalic structures comprised most of the characters used in the analysis. Multiple state characters were used to construct the original data matrix. Hennig 86 allows two-way transformation series; the character coding in the data matrix (Table 2) and the character descriptions given below



TABLE 2. Data matrix. Column = characters, 0 = plesiomorphic state, 1, 2, 3, 1', 2' = derived states; row = genera: EUA, *Euaspa* (outgroup); JAP, *Japonica* (outgroup); CHR, *Chrysozephyrus*; THE, *Thermozephyrus*; NEO, *Neozephyrus*; SIB, *Sibataniazephyrus*; QUE, *Quercusia*; FAV, *Favonius* excluding *F. saphirinus*; FAS, *Favonius saphirinus*; AUS, *Austrozephyrus*.

	1	2	3	4	5	6	7	8	9	1 0	1 0	1 2	1 3	1 4	1 5	1 6	1 7
JAP	0	0	0	1'	0	0	0	0	0	0	0	0	0	0	0	0	0
EUA	0	0	0	0	0	0	0	0	0	1	0	1'	0	0	1	0	0
CHR	2	1	0	0	0	0	0	0	0	0	0	1	2	1	1	0	1
THE	3	1	0	0	0	0	0	0	1'	0	0	1	2	1	1	0	1
NEO	1	1	0	1	0	0	0	0	0	0	1	1	2	1	1	0	1
SIB	0	1	0	0	1	0	1	1	0	0	0	0	2	0	1	0	1
QUE	2'	1	0	2'	0	0	1	0	1	0	0	0	1	0	1	1	1
FAV	1'	1	0	2	0	0	0	0	2	0	1'	0	2	1	1	0	1
FAS	0	1	0	2	0	0	0	0	2	0	1'	0	2	1	1	1	1
AUS	0	2	1	0	0	1	0	0	0	1	0	1	2	1	1	0	1

are two-way. When PAUP was used, all the characters with two-way transformation series were divided into two characters with one-way transformation series.

We polarized the characters mainly by outgroup comparisons. When the plesiomorphic state was not assigned to outgroups, explanations are followed by the character descriptions. In all character descriptions, the presumed plesiomorphic state (0) is listed first, followed by a transformation series in one direction (1, 2, . . .) and a transformation series in another direction (1', 2', . . .) respectively, when necessary.

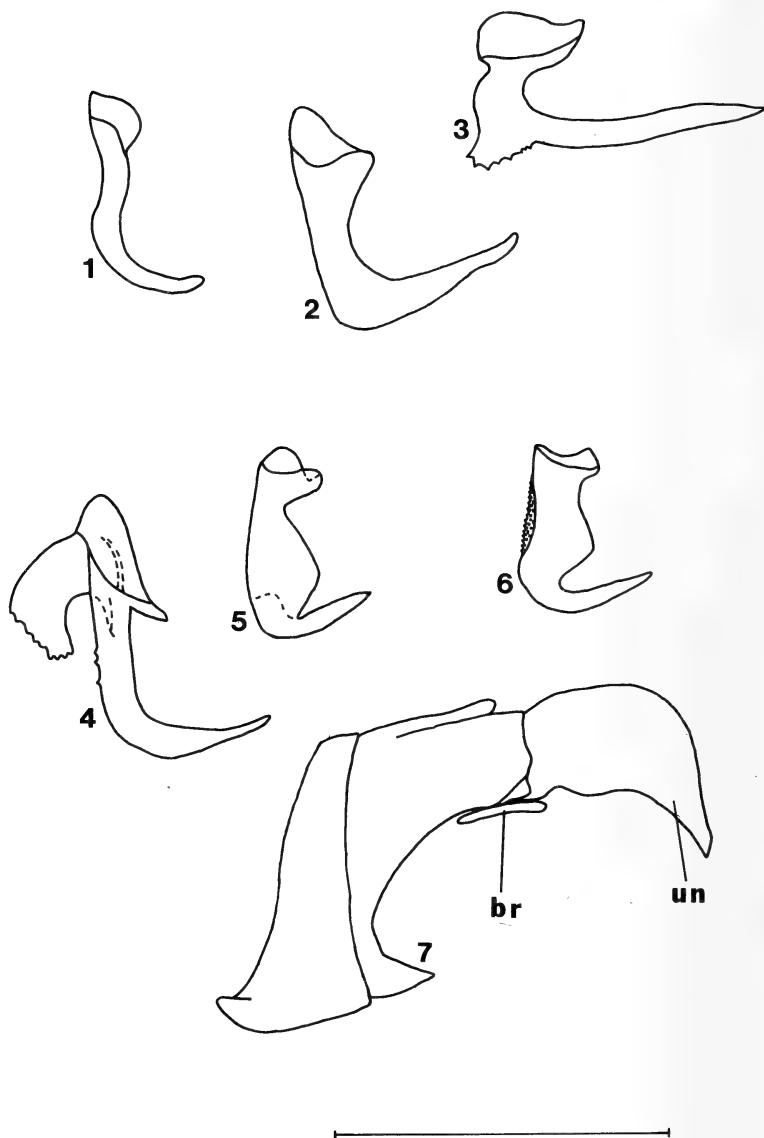
1. Brachium on tegumen: smooth and simple (Figs. 1, 24, 29) (0); smooth but flattened (Fig. 2) (1); serrated anteriorly (Fig. 3) (2); similar to state 2 but with additional large serrated lobe extending anteriorly (Fig. 4) (3); smooth, with basal half enlarged (Fig. 5) (1'); similar to state 1' but bearing numerous minute teeth in front (Fig. 6) (2').

2. Articulation of brachium with tegumen: double-articulated (0); single-articulated (1); brachium fused with tegumen, no articulation (2).

3. Brachium general shape: hook shape (Figs. 1–6) (0); rod shape (Fig. 7) (1).

4. Phallus structure: symmetrical with no special modification (Fig. 8) (0); generally symmetrical but bearing an elongate dentate sclerite at the right side of aedeagus (Fig. 10) (1); similar to state 1 but dentate sclerite reduced with left side of aedeagus also reduced (Fig. 11) (2); caudal end of aedeagus slightly asymmetrical, weakly sclerotized (Fig. 12) (1'); caudal end of aedeagus strongly asymmetrical, forming complicated, heavily sclerotized structure (Fig. 13) (2').

The character state (1') of *Japonica* was considered derived because



FIGS. 1-6. Left brachium: 1, *Japonica saepestriata*; 2, *Neozephyrus japonicus*; 3, *Chrysozephyrus smaragdinus*; 4, *Thermozephyrus ataxus*; 5, *Favonius orientalis*; 6, *Quercusia quercus* (scale line = 1 mm).

FIG. 7. Lateral view of sclerites of 9 + 10 genitalic segments with modified left brachium attached in *Austrozephyrus obsolon*; br, brachium, un, so-called "uncus" with its homology with the other uncus-like structures found in the other Theclini uncertain (scale line = 1 mm).

the simple, symmetrical phallus (0) is found commonly in ingroup genera and also in the other outgroup genus *Euaspa*.

5. Phallus upcurved: no (Fig. 9) (0); yes (Figs. 25, 30) (1).

6. Aedeagus twisted: no (Figs. 8, 10–13) (0); aedeagus twisted 90° toward the left side (Fig. 14) (1).

7. Juxta shape: U- or V-shaped (Figs. 15, 16) (0); modified into a simple plate (Figs. 17, 26, 31) (1).

8. Harpal region of valva: no process (Figs. 18–21) (0); bearing a prominent elongate process proximately (Figs. 27, 32) (1).

9. Ampulla of valva: not serrated (Figs. 18, 27, 32) (0); finely serrated mesad (Fig. 19) (1); strongly serrated mesad (Fig. 20) (2); modified into a large erect, dentate tooth (Figs. 21, 22) (1').

10. X tergite: uncus absent (Figs. 23, 28) (0); so-called "uncus" (with homology uncertain) in various forms present (Fig. 7) (1).

The plesiomorphic state was not assigned to the so-called "uncus" found in *Euaspa* because this uncus-like structure is found only in *Austrozephyrus* in the ingroup and its homology with *Euaspa* was uncertain. This decision is supported by the fact that both Ogyrini and Arhopalini, the most likely sister groups of Theclini, lack an uncus (Eliot 1973).

11. Two signa on corpus bursa: small, rounded, invaginated inwards into a spine (Figs. 35, 36, 38) (0); extended enormously into a spiny, elongate stripe (Fig. 34) (1); lost (Fig. 33) (1').

12. Lamella postvaginalis of sterigma: bilobed, separated into two pieces (Figs. 33, 36, 38) (0); modified into a single rectangular plate, sometimes with complicated structures (Fig. 34) (1); modified into a double layered plate, with the ventral layer elongate and rectangular while the dorsal layer bifid, finger-like, and projecting posteriorly (Fig. 35) (1').

The character state (1') of outgroup *Euaspa* is apparently not plesiomorphic since this state is specific to *Euaspa* and not found anywhere else in Theclini.

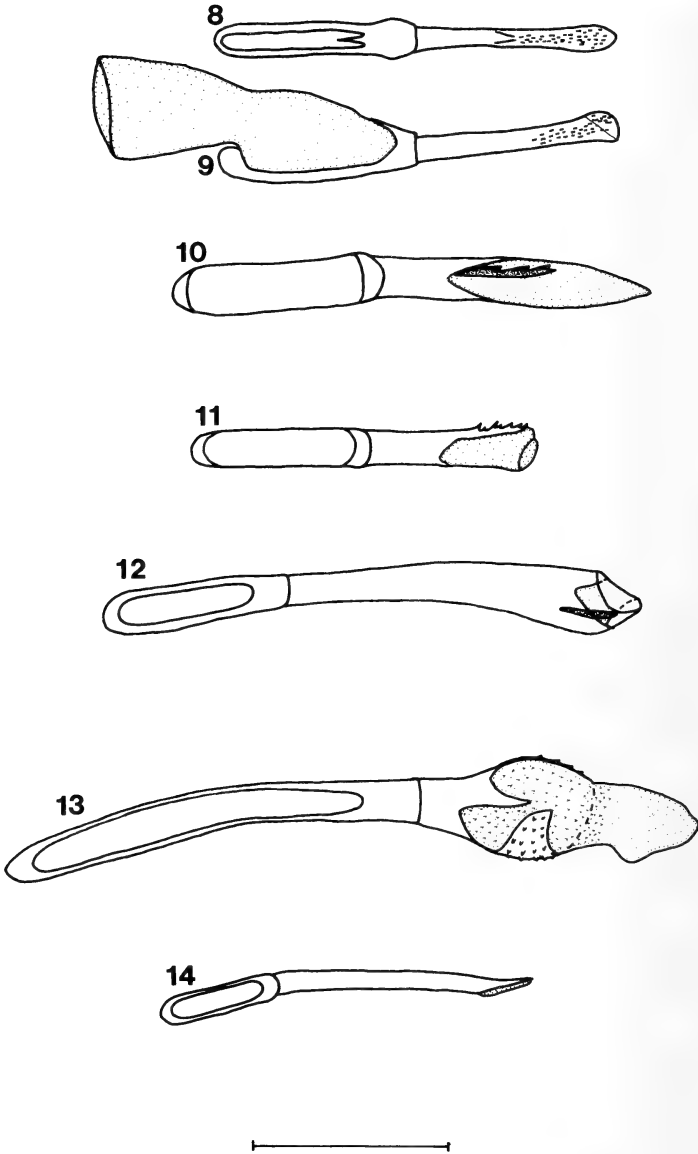
13. Sexual dichromatism: absent (0); present, male with specialized purple metallic scales on upperside of the wings, female dull-colored (1); similar to state 1 but with green/blue metallic scales (2).

14. Female polymorphism: absent (0); present, individual with blue patch, orange spots, or both present or absent on forewing upperside (1).

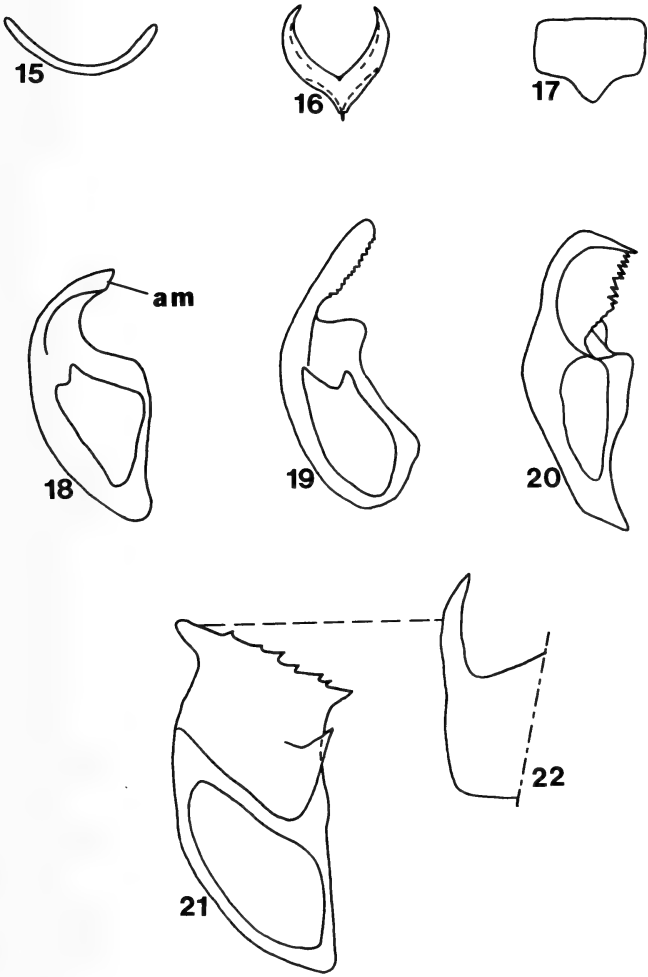
15. Foretarsus: segmented in both sexes (0); rudimentary in male (1).

16. Forewing venation: M1 forked with R3 away from the base (0); M1 forked with R3 at the base (1).

17. Male eyes: naked or sparsely hairy (0); densely hairy (1).

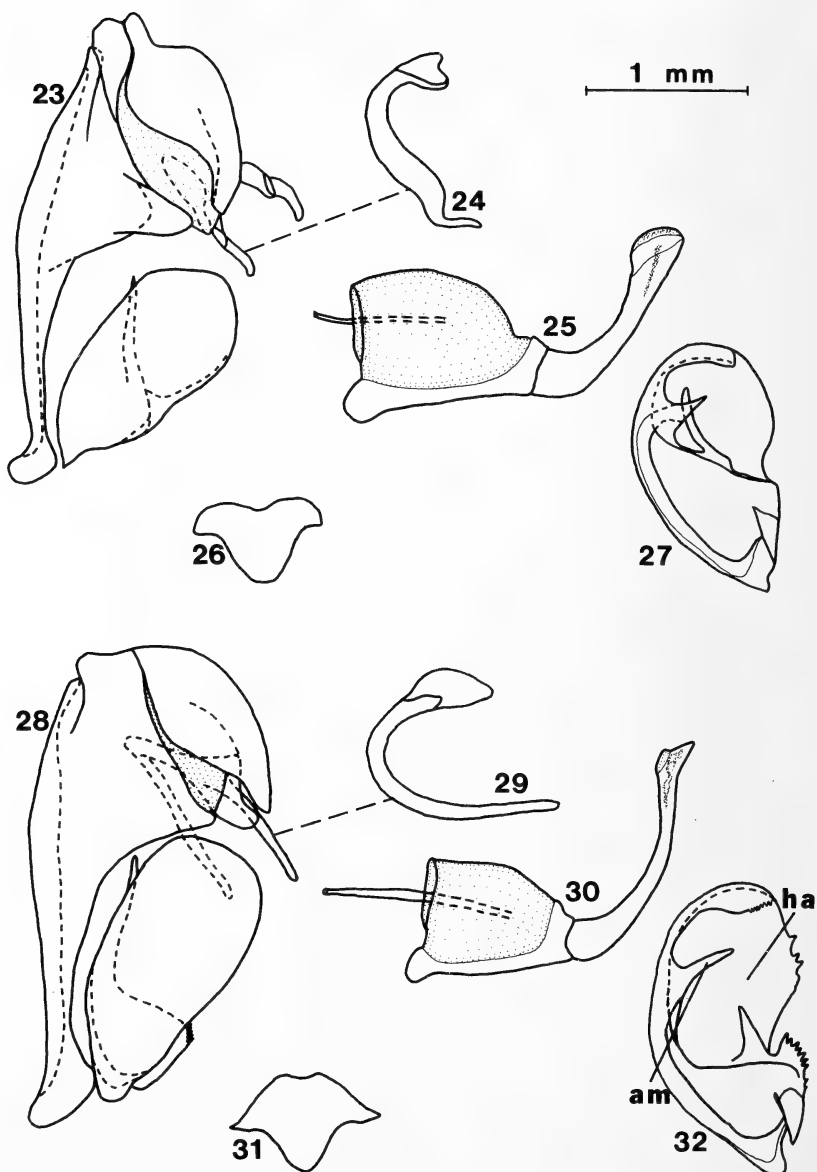


FIGS. 8-14. Phallus: 8, *Chrysozephyrus smaragdinus* (dorsal view); 9, *Chrysozephyrus smaragdinus* (ventral view); 10, *Neozephyrus japonicus*; 11, *Favonius orientalis*; 12, *Japonica saepestriata*; 13, *Quercusia quercus*; 14, *Austrozephyrus obsolon* (scale line = 1 mm).



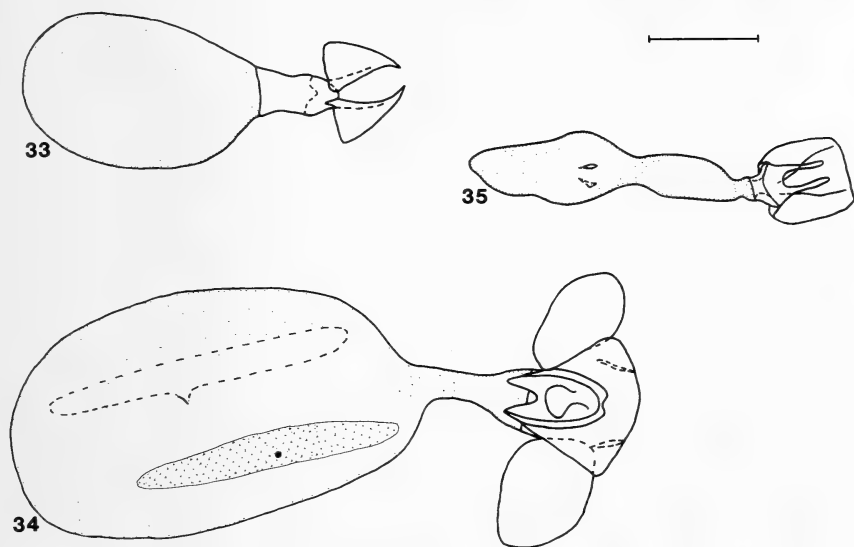
FIGS. 15-17. Juxta: 15, *Japonica saepestriata*; 16, *Chrysozephyrus smaragdinus*; 17, *Quercusia quercus* (scale line = 1 mm).

FIGS. 18-22. Right valva: 18, *Chrysozephyrus smaragdinus*; 19, *Quercusia quercus*; 20, *Favonius orientalis*; 21, *Thermozephyrus ataxus*; 22, Lateral view of right ampulla of *Thermozephyrus ataxus* (scale line = 1 mm).



FIGS. 23-27. Male genitalia of *Sibataniozephyrus fujisanus* (Matsumura): 23, Lateral view of sclerites of 9 + 10 genitalic segments with brachia and left valva attached; 24, left brachium; 25, phallus; 26, juxta; 27, dorsal view of right valva.

FIGS. 28-32. Male genitalia of *Sibataniozephyrus kuafui*, new species: 28, Lateral view of sclerites of 9 + 10 genitalic segments with brachia and left valva attached; 29, left brachium; 30, phallus; 31, juxta; 32, dorsal view of right valva.



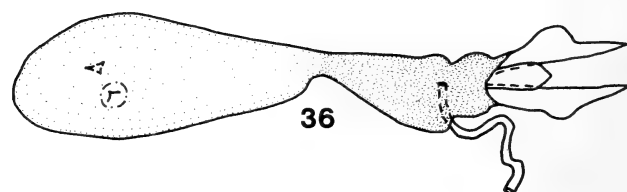
FIGS. 33–35. Female genitalia: **33**, *Favonius jezoensis*; **34**, *Neozephyrus taiwanus*; **35**, *Euaspa milionia* (scale line = 1 mm).

#### RESULTS OF THE CLADISTIC ANALYSES

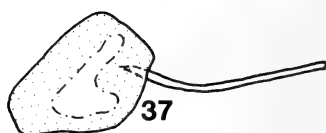
Two minimum length trees (Figs. 40, 41) were derived from the data set using Hennig 86 each with  $CI = 0.78$ . Two equally parsimonious trees of the same topologies as above were found using PAUP each with  $CI = 0.81$ . The ingroup topology did not change when the outgroups were removed.

The high  $CI$  values of the trees ( $CI = 0.78/0.81$ ) indicate that the data matrix has relatively little homoplasy.

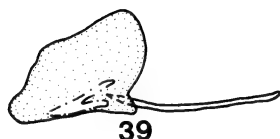
*Austrozephyrus*, considered by Saigusa (1983) to be closely related to *Euaspa*, forms a monophyletic clade with *Quercusia* lineage distinct from *Euaspa*, supported by characters 2, 13, and 17 (Figs. 40, 41). Thus it should be retained within the ingroup. Whether *Sibatanozephyrus* should be treated as congeneric with *Quercusia* is still somewhat disputable. Of the two equally parsimonious trees produced, one suggests a monophyletic relationship between *Sibatanozephyrus* and *Quercusia* (Fig. 40). Nevertheless this tree seems less likely to reflect the true phylogeny because the only synapomorphy for the two genera is a platelike juxta (character 7). With the rest of the ingroup and outgroup genera possessing a V- or U-shaped juxta, the platelike juxta found in *Sibatanozephyrus* and *Quercusia* may reflect the loss of function owing to the specialized phallus of the two genera. The strongly upcurved phallus of *Sibatanozephyrus* and the elongate phallobase and enlarged



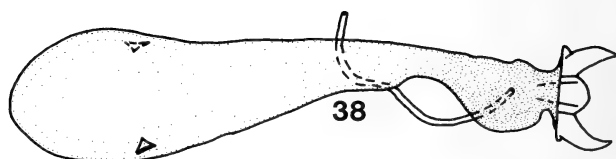
36



37



39



38

1 mm

FIGS. 36–37. Female genitalia of *Sibataniozephyrus fujisanus* (Matsumura): **36**, Corpus bursae with stigma; **37**, papilla analis with apophysis posterioris.

FIGS. 38–39. Female genitalia of *Sibataniozephyrus kuafui*, new species: **38**, Corpus bursae with stigma; **39**, papilla analis with apophysis posterioris.

aedeagus of *Quercusia* probably function to stabilize the phallus in the male genitalic complex. Thus it is our view that the platelike juxta can not be regarded unequivocally as a synapomorphy for these two genera. Furthermore, this tree suggests the most derived state of character 13 (i.e., metallic blue/green color in male) evolved twice: once on the lineage of *Sibataniozephyrus* and the other on the lineage leading to



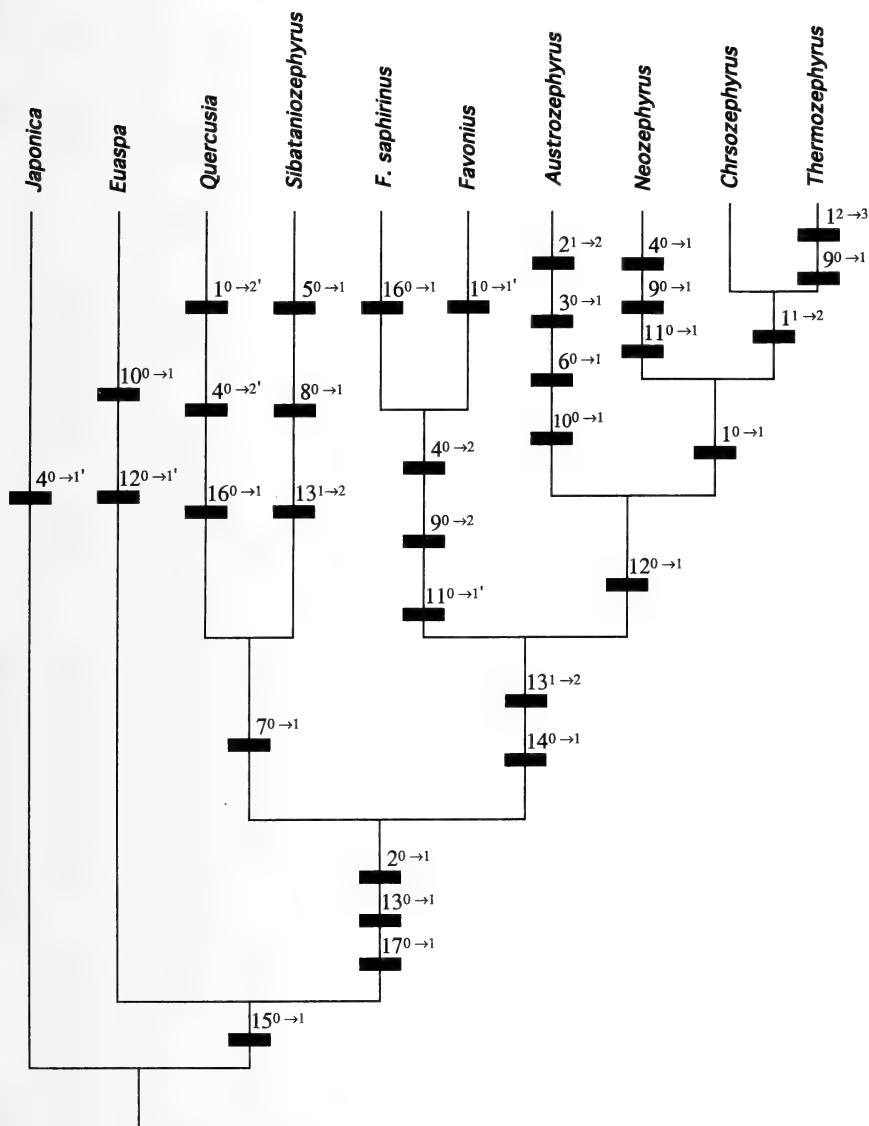


FIG. 40. A cladogram less likely to reflect the true phylogeny of *Sibataniaozephyrus* and possibly related genera (produced primarily by Hennig 86 but with slight modification at the base since character 15 is more logical to have segmented tarsus assigned as plesiomorphic state).

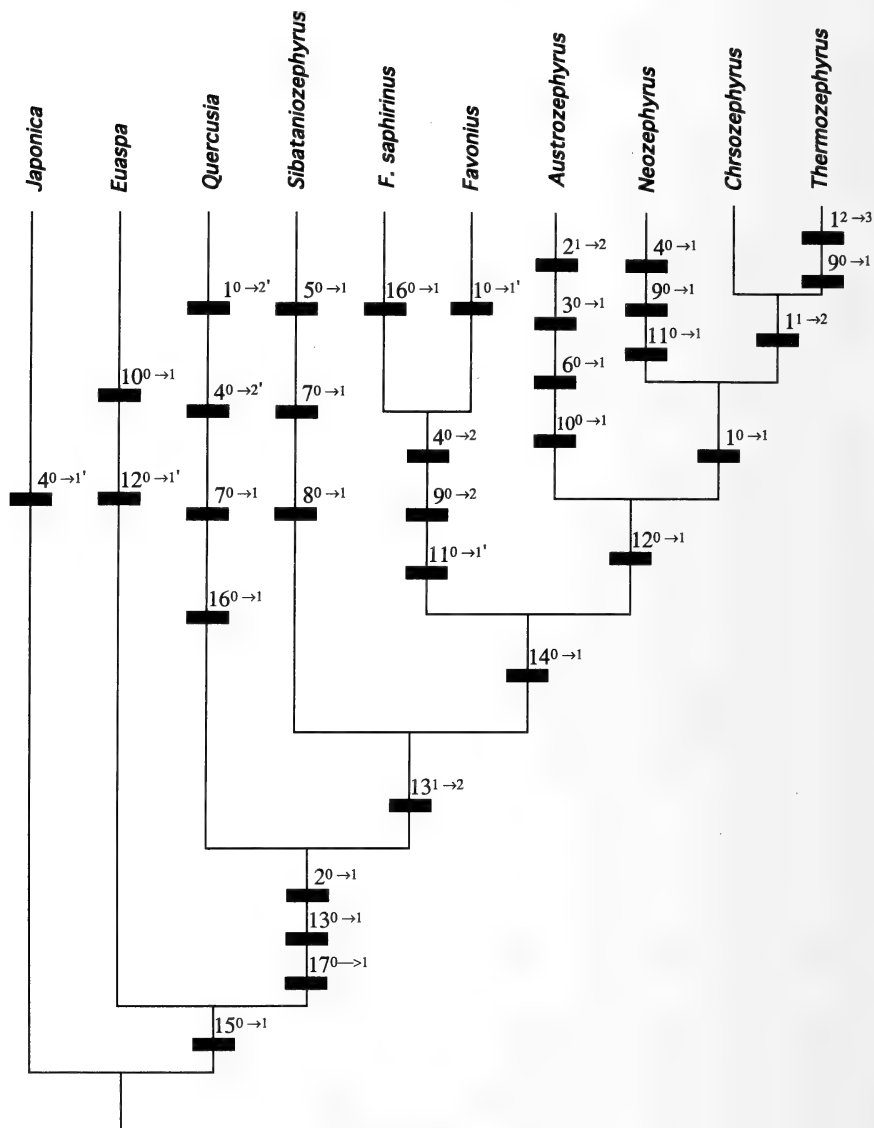


FIG. 41. Proposed phylogeny based upon the preferred cladogram for *Sibataniozephyrus* and possibly related genera (produced primarily by Hennig 86 but with slight modification at the base since character 15 is more logical to have segmented tarsus assigned as plesiomorphic state).

the rest of the metallic green/blue-winged genera. However, because *Sibatanozephyrus* and the majority of the other blue/green-winged genera are found in the same geographical range in Asia and not found in the other continents where Theclini also are present, the metallic green/blue scales probably evolved only once. The cladogram shown on Fig. 41 shows a paraphyletic relationship between *Quercusia* and *Sibatanozephyrus*. Both genera have a few autapomorphies which justify their separation as genera in the annotated Linnaean classification conventionally used. *Quercusia* possesses characters 1, 4, 16 and *Sibatanozephyrus* characters 5 and 7.

It is our view that *Sibatanozephyrus* should be recognized as an independent genus and the superficially similar platelike juxta is homoplastic. Based on the preferred proposed phylogeny, the purple *Quercusia* is a sister group of all the other genera having metallic green or blue scales in the male. All these green/blue-winged genera are found only in east and southeast Asia; *Quercusia* and the green/blue-winged genera are allopatric. It seems that *Quercusia* diverged early in the evolutionary history of these groups and extensive evolutionary change took place between the two lineages. *Sibatanozephyrus* also diverged early and underwent significant specialization as it obtained its unique niche of *Fagus*-feeding, a feature found nowhere else in Theclini. These specializations probably occurred after the lineage of the common ancestor of the green/blue-winged genera already split from the lineage of the ancestor of *Quercusia*, which feeds on a wide range of plants in different families but is not known to feed on European *Fagus* (Shirôzu 1961, Carter 1982). It is apparent that symplesiomorphic characters shared by these two lineages of Theclini led to Shirôzu and Yamamoto's (1956) decision to treat them as congeneric.

#### TAXONOMY

##### *Sibatanozephyrus* Inomata, 1986

*Sibatanozephyrus* Inomata 1986:120.

**Type-species.** *Zephyrus fujisanus* Matsumura, 1910, by monotypy. Gender masculine.

**Diagnosis.** Moderate sized, diurnal butterflies (FW length 15.0–18.6 mm). **Head:** Hairy, clothed with upraised, black and grayish white hairs on vertex and frons, appressed scales on occiput, a white rim surrounding the eye; eye semi-oval, hairy; labial palpus hairy, porrect, pointed, projecting ahead of plane of front; maxillary palpus reduced, not visible; proboscis unscaled; antenna smooth-scaled, with projecting setae at nudum in both sexes, antennal length in male longer than in female. **Thorax:** Grayish white dorsally, tinged with metallic structural colors under reflection of light in male, uniformly brown in female; white ventrally, legs white, banded with dark brown on tarsi. **Abdomen:** Dark brown dorsally, white ventrally. **Forewing:** Termen nearly straight, costa curved; 11 veins, R4 + 5 and M1 both forked with R3, the forking points dividing R3 into three nearly equal long parts; upperside scaling shining metallic with a dark dull margin in male, uniformly dark in female, both sexes with underside markings visible by transparency; underside scaling white to pale brown with series of dark submarginal spots between two

transverse lines; a prominent dark discal band, a white patch between this band and the submarginal spot system regardless of ground color. Fringe white. **Hindwing:** Slender "tail" from Cu2; 9 veins all separate; upperside scaling shining metallic with a dark margin always broader than that of forewing in male, uniformly dark in female, both sexes with a very fine white outline along termen, underside markings visible by transparency; underside scaling similar to that of forewing but with a large yellow or orange tornal patch with black rounded spot in Cu1, and a black irregularly shaped spot at the tornus, white outline also present; "tail" black with white tip on both surfaces. Fringe generally white, but outer fringe around tornus dark brown. **Male genitalia:** Sclerites of 9th and 10th segments fused into a complete ring, with tegumen of two segments indistinguishable; uncus absent; socii folded deeply inwards; brachium single-articulated with tegumen, smooth, hook-like; saccus fairly short; phallus symmetrical, strongly upcurved; juxta platelike; valva semicircular, ampulla forming a long spine, harpal region bearing a slender process proximally, fused with the lobelike cucullus + valvula distally, costa prominent and elongate, sacculus relatively well developed with a solid ventral ridge. **Female genitalia:** Apophyses posteriores elongate, slender, with weakly sclerotized, somewhat square-shaped papillae anales; ductus bursa slender, heavily sclerotized; sterigma with lamella antevaginalis absent, lamella postvaginalis heavily sclerotized, forming a pair of spines projecting posteriorly; corpus bursa oval, bearing a pair of small, invaginated spinelike signa.

### Biology of *Sibatanozephyrus*

The biology of *S. fujisanus* has been described in detail by Shirôzu and Hara (1960) and Fukuda et al. (1984). It will be briefly summarized below because both works are in Japanese. The exclusive host plants of *S. fujisanus* are *Fagus crenata* Blume and *F. japonica* Maximowicz. Ovum is white and fairly large (diameter 1.00–1.02 mm, height 0.54 mm). It is laid singly on a twig and hibernates. The larva hatches in early spring when the host starts budding, and initially bores into buds. The fully grown larva is yellowish brown, reaching 16.5 mm. It makes a shelter by spinning two or three leaves together, and consumes young leaves and buds. Feeding usually takes place nocturnally. The pupa is uniform light brown with two rows of subdorsal dark dots. Pupation usually takes place under fallen leaves around the base of the host. *Sibatanozephyrus kuafui*, the new species described below, presumably feeds on *F. hayatae* Palibin ex Hayata because this butterfly is associated exclusively with this plant.

### *Sibatanozephyrus fujisanus* (Matsumura)

(Figs. 23–27, 36, 37, 42–45)

*Zephyrus fujisanus* Matsumura 1910:221.

*Zephyrus nohirae* Matsumura 1915:1, pl. 1, fig. B.

*Zephyrus attilia* ab. *subgriseus* Wileman 1911:55.

*Zephyrus fujisanus* ab. *yamamotoi* Uchida 1932:232, tab. 16, fig. 5.

*Zephyrus fujisanus* ab. *zoasanus* Kanda 1933:8.

*Favonius fujisanus*; Sibatani & Ito 1942:327.

*Quercusia fujisanus*; Shirôzu & Yamamoto 1956:393.

*Quercusia fujisanus latimarginatus* Murayama 1963:48, figs. 31, 33, 35, 37. syn. n.

*Sibatanozephyrus fujisanus*; Inomata 1986:120 (synonymy).

TL. Mt. Fuji [Honshu, JAPAN].

**Diagnosis. Male:** Forewing length 16.0–18.0 mm (mean = 17.0 mm,  $n = 3$ ); antennal length 8.0–8.8 mm (mean = 8.35 mm,  $n = 3$ ). Forewing upperside bright metallic bluish green, margin dark brown; underside ground color yellowish white or white tinged with brown, all markings brown with a very stout transverse line adjacent and proximal to the submarginal spots. Hindwing upperside with coloration similar to that of forewing but with a much broader dark brown margin, its narrowest part still wider than the broadest part of the forewing margin, the white outline weakly developed; underside with the same ground color as forewing, discal band and discoidal bar separate, tornal patch yellow. **Male genitalia:** Ring-shaped sclerites of 9 + 10 segments width 0.56 times height; tegumen 9 + 10 forming a bump dorsally; brachium twisted; phallus with a short, stout aedeagus, length 1.1 times phallobase; valva with a short spine on ampulla, 0.2 times as long as entire valva, distal margin of the harpal region and ventral ridge of sacculus smooth, not serrated.

**Female:** FW length 15.0–17.2 mm (mean = 16.5 mm,  $n = 8$ ); antennal length 7.0–7.8 mm (mean = 7.2 mm,  $n = 8$ ). Both wings with upperside ground color uniformly brown, underside pale brown with an orange tornal patch, otherwise similar to male. **Female genitalia:** Lamella postvaginalis spines long and slender, each with a semicircular lateral lobe near the base, arranged nearly parallel to each other, with distance between the tip of the two spines approximately 0.19 mm; distance from the tip of the spine to ostium 0.53 mm; ostium width 0.01 mm.

**Species examined.** JAPAN: 2♀, Honshu, Tottori Pref., Mt. Daisen, 25. VI. 1973 (T. Yuzuriha); 1♂1♀, same locality as above, 25. VI. 1983 (Y. Hama); 1♂2♀, Honshu, Kyoto Pref., Mt. Oe, emgd. 11. V., 15. V. and 27. V. 1983 (S. Kugo); 1♀, Honshu, Kyoto Pref., Tamba Town, Funai-gun, emgd. 10. V. 1977 (T. Yuzuriha); 1♀, Honshu, Kyoto Pref., Asauegun, Yamakawamachi, Mt. Kouetsu, emgd. 14. V. 1984 (T. Yuzuriha); 1♂, Yamanashi Pref., Tomurozawa, emgd. 15. V. 1984 (T. Yuzuriha); 1♀, Hokkaido, Kaminokunicho, Zentana, emgd. 3. VI. 1986 (T. Doi).

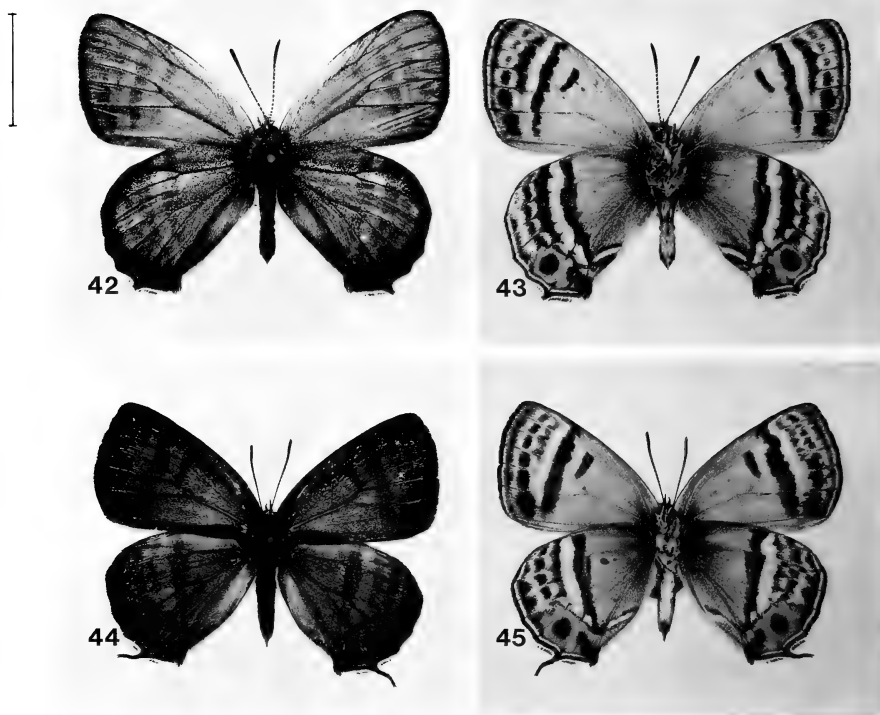
**Geographical distribution.** *S. fujisanus* is endemic to Japan (southern Hokkaido, Honshu, Shikoku, and northern to central Kyushu).

**Comments.** The populations in Kyushu, southern Japan, have been given subspecific status based upon two characters: the broader dark margin on upperside of the wings and the darker color on the underside of the wings. However, Inomata's (1986) discussion and numerous pictures of samples from various regions in Japan clearly reveal that variation within the two traits is continuous. The southern populations have a stronger tendency to show the two traits, but specimens indistinguishable from those from central Japan are encountered. This is clearly an example of clinal variation and in our opinion should not be recognized nomenclaturally.

### *Sibatanozeephyrus kuafui* Hsu & Lin, new species

(Figs. 28–32, 38, 39, 46–49)

**Description. Male:** Forewing length 16.1–18.6 mm (mean = 17.08,  $n = 24$ ); antennal length 8.2–9.0 mm (mean = 8.5 mm,  $n = 24$ ). Forewing upperside metallic dark blue tinged with green, margin black; underside ground color white with submarginal spots dark black, other markings dark gray, the proximal transverse line very slim. Hindwing upperside with the metallic area greenish blue with a purplish outline, margin black, not as broad as in *S. fujisanus*, the terminal outline distinct, forming a white line through entire termen; underside with the same ground color as of the forewing, discal band and discoidal bar always completely merged, not distinguishable from each other, tornal patch orange or yellowish orange. **Male genitalia:** Ring-shaped sclerites of 9 + 10 segments width 0.65 times height; tegumen 9 + 10 with dorsal side flat; brachium forming a simple hook, not twisted as in *S. fujisanus*; phallus with a long and slender aedeagus, length 1.4 times phallobase; valva with a long spine on ampulla, 0.3 times as long as entire valva, distal margin of the harpal region bearing 4 to 10 teeth ( $n = 9$ ), number not always equal on opposite valvae, ventral ridge of sacculus heavily serrated.



FIGS. 42–45. *Sibatanozephyrus fujisanus* (Matsumura) (JAPAN, Honshu): 42, ♂, upperside; 43, ♂, underside; 44, ♀, upperside; 45, ♀, underside (scale line = 1 cm).

**Female:** Forewing length 16.0 mm ( $n = 1$ ); antennal length 7.0 mm ( $n = 1$ ). Both wings with upperside ground color dark brown and underside markings more developed than those in the male, otherwise similar to the male. **Female genitalia:** Lamella postvaginalis spines short and stout, no lateral lobe; the two spines widely separated, diverging, distance between tips of the two spines approximately 0.46 mm; distance from the tip of the spine to ostium 0.30 mm; ostium width 0.01 mm.

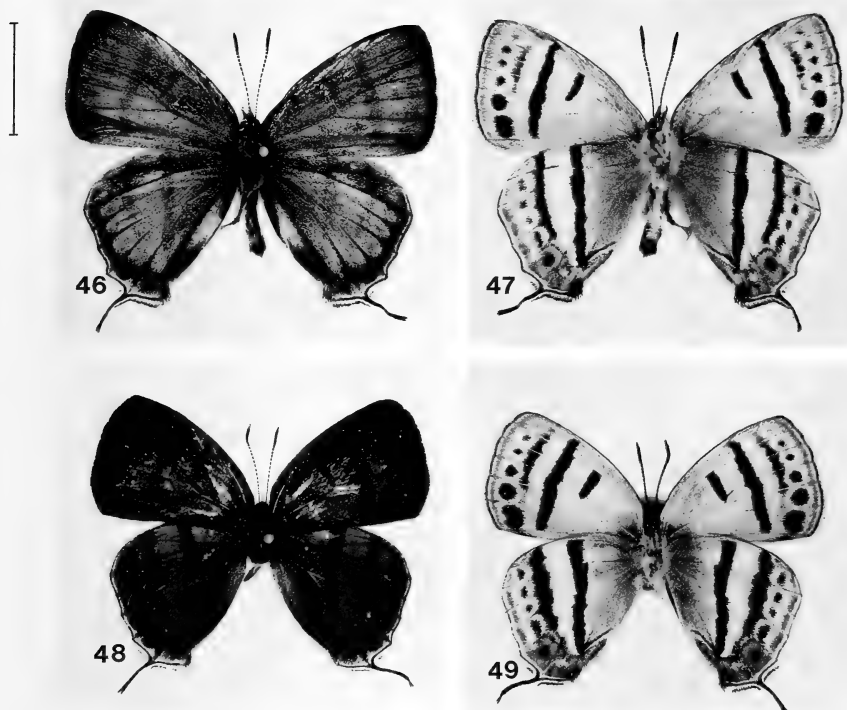
**Type material.** Holotype ♂, TAIWAN: Taipei Hsien, Sanhsia, Mt. N. Chatienshan, 1700–1727 m. 121°27'E, 24°47.5'N, 22. V. 1993 (Y. F. Hsu & M. Y. Lin) (NTUIM). Paratypes. 9♂1♀, same data as holotype (1♀ dissected: Genitalia YFH 0747); 14♂, same locality as holotype, 28/29. V. 1992 (9♂ dissected: Genitalia YFH 0441, 0442, 0447, 0487, 0498, 0499, 0500, 0501, 0502) (Y. F. Hsu & M. Y. Lin) (BMNH; CAS; IZASB; NTUIM; UCB; NMNH).

**Depositories.** Abbreviations of institutions are as follows: the Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Zoological Institute of Academia Sinica, Beijing (IZASB); the Insect Museum, National Taiwan University, Taipei (NTUIM), Essig Museum of Entomology, University of California, Berkeley (UCB), and U.S. National Museum of Natural History, Washington, D.C. (NMNH).

**Geographical distribution.** *S. kuafui* is known from Taiwan.

**Etymology.** Kuafu is a character in Chinese mythology who tried to challenge the sun by chasing it until his exhausting death.

**Comments.** *Sibatanozephyrus kuafui* undoubtedly utilizes *Fagus hayatae* as its larval host in Taiwan because it is associated exclusively with this plant. *Fagus hayatae*, formerly



FIGS. 46–49. *Sibatanozephyrus kuafui*, new species (TAIWAN): 46, ♂, upperside; 47, ♂, underside; 48, ♀, upperside; 49, ♀, underside (scale line = 1 cm).

recognized as Taiwan endemic, recently has been reported from central China and was noted by Shen and Boufford (1988) as a remarkable new example of disjunction between Taiwan and central China. This discovery suggests that the population of *S. kuafui* in Taiwan may be a relict and suggests the possibility of finding this insect on mainland China. Shen and Boufford (1988) also point out that *F. lucida* and *F. hayatae* are more closely related to each other than they are to any other extant species of *Fagus*. According to Tsien et al. (1975:11), *F. lucida* is distributed approximately between 24°N and 30°N, which covers the latitudinal range where *F. hayatae* and *S. kuafui* are found in Taiwan. This fact makes *F. lucida* another candidate as a larval host for *S. kuafui*, or a possible sister species, on the Chinese mainland because this beech is apparently far more abundant than *F. hayatae* there.

#### CONCLUSION AND DISCUSSION

We conclude that *Sibatanozephyrus* should be considered a valid genus distinct from *Quercusia* on the basis of their phylogenetic relationship, biology, and biogeography. Each of these two genera retains several symplesiomorphic characters, while each has gained autapomorphic features. This phenomenon led early workers to lump them into a single genus.

We predict that *Sibatanozephyrus* will eventually be found on mainland China because China supports the richest diversity of both *Fagus* and Theclini in the world (Table 1). Moreover, it seems likely that more than one *Sibatanozephyrus* species may be present on mainland China based on the following observations:

1) There are multiple species of *Fagus* in China, and these species show various degrees of allopatry. Even when multiple species are sympatric, each species usually is dominant in a different topogeographical and horizontal zone (Tsien et al. 1975), which might favor vicariant speciation because relictual *Fagus* populations may function as isolated ecological and evolutionary islands.

2) Pollen studies reveal that *Fagus* species lived in many areas where they are absent today (Steenis 1971) indicating *Fagus* populations have suffered extensive extinctions in the past, which also may have led to vicariant speciation.

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## AVIAN PREDATION ON THE MONARCH BUTTERFLY, *DANAUS PLEXIPPUS* (NYMPHALIDAE: DANAINAE), AT A CALIFORNIA OVERWINTERING SITE

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**ABSTRACT.** Avian predation on monarch butterflies (*Danaus plexippus* L.) was observed at a California monarch overwintering site. A pair of rufous-sided towhees (*Pipilo erythrophthalmus* Linnaeus) exerted a 6.51-7.43% annual mortality on the overwintering colony, consuming an average of 22.7 butterflies/day. A characteristic predatory signature was observed on the uneaten remains left by the towhees. Tagging studies indicate that tagged butterflies were at greater risk of predation than were untagged butterflies.

**Additional key words:** rufous-sided towhee, sex ratios, cardenolides, tagging.

There are several reported examples of predation of monarch butterflies at overwintering sites. In Mexico, avian predators include black-headed grosbeaks (*Pheucticus melanocephalus* Swainson), Scott's oriole (*Icterus parisorum* Bonaparte), and black-backed oriole (*Icterus abeillei* Lesson) (Calvert et al. 1979, Brower & Calvert 1985). In California, avian predators include chestnut-backed chickadees (*Parus rufescens* Townsend) (Tuskes & Brower 1978, Brower & Fink 1985, Bell & Dayton 1986), starlings (*Sturnus vulgaris* L.) (Dayton & Bell, pers. comm.), and scrub jays (*Aphelocoma coerulescens* Bosc) (Peterson, pers. comm.). Mammalian predators found at Mexican overwintering sites include *Peromyscus spicilegus* J. A. Allen, *Microtus mexicanus salvus* Hall, and *Peromyscus melanotis* (= *P. maniculatus labecula* Elliott) (Brower et al. 1985, Glendinning et al. 1988). Leong et al. (1990) reported monarch predation in California by yellowjackets (*Vespula vulgaris*). In the 1989-90 season, I discovered a pair of rufous-sided towhees (*Pipilo erythrophthalmus* Linnaeus, Emberizidae) preying upon monarchs in a moderate-sized overwintering colony in the Santa Monica Mountains, Los Angeles County, California. During the course of tagging monarch butterflies at this site, I measured predation rates.

### METHODS

From 13 September 1989 to 28 March 1990, I made weekly visits to a monarch overwintering site along the coast in Los Angeles County, California, 18 km west of Malibu, to tag monarch butterflies. Tags of the type developed by Urquhart (1960, 1976, 1987) were used to de-

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TABLE 1. Observations of a single pair of rufous-sided towhees feeding activities on 31 January 1990.

Time	Activities observed
06:53 h	Sunrise (Anon 1989).
07:00 h	Unsuccessful sally.
07:03 h	Unsuccessful sally. Monarch flies, bird sally-strikes unsuccessfully.
07:08 h	Successful sally.
07:13 h	Successful sally.
07:45 h	Sunlight hitting site. No bird activity.
08:03 h	Picks up monarch fallen on ground.
08:07 h	Picks up monarch fallen on ground.
08:13 h	Successful sally.
08:15 h	Picks up monarch fallen on ground.
08:27 h	Picks up monarch fallen on ground.
08:30 h	Successful sally, does not eat it.
08:31 h	Successful sally.
08:51 h	Successful sally.
09:01 h	Successful sally.
No bird activity after this.	

termine predation rate and selectivity. All butterfly remains were collected from the litter under the clustering areas during my weekly visits. On 12 and 13 January 1990, the site was visited, and butterfly remains were collected to measure daily predation rate.

Field observations of bird predation were made by binoculars. Continuous early morning observations from before sunrise until no further predation activity was observed were made on three occasions. Because rufous-sided towhees are not sexually dimorphic, I was unable to distinguish between the sexes. Terms used to describe monarch predation by towhees follow Remsen and Robinson (1990).

## RESULTS

Towhee activity recorded on 31 January 1990 is presented in Table 1. The pair of towhees "perched" on small shrubs. Looking about, the towhee would "sally" up some 10–15 m into the tree, "pounce" upon a butterfly, and bring it to the ground near or under a shrub. On other occasions, the attacked butterfly fell to the ground, where the bird would pick it up. The towhee also attacked monarchs that previously had fallen to the ground. It appears that the towhee "snips" the butterfly between the head and thorax based on examination of intact dead butterflies. All four wings were removed by the bird by "snipping" between the body and wing and "shaking" the prey until the wings fell off before the body was consumed. Characteristic piles of the four wings were often found under or near shrubbery.

TABLE 2. Tagging and recapture summary KSP site in 1989-90.

Date	♂ tagged	♀ tagged	Total tagged	% ♂	Recaptures	Recap % ♂	Total captured
4 Oct 89	3	1	4	75.0	0	0	4
11 Oct 89	22	1	23	95.7	1	100	24
18 Oct 89	63	41	104	60.6	4	100	108
25 Oct 89	180	124	304	59.2	32	71.9	336
1 Nov 89	157	124	281	55.9	11	45.5	292
13 Nov 89	242	219	461	52.5	15	60.0	476
15 Nov 89	173	204	377	45.9	57	61.4	434
22 Nov 89	249	225	474	52.5	36	61.1	510
29 Nov 89	135	115	250	54.0	30	70.0	280
6 Dec 89	58	50	108	53.7	17	64.7	125
13 Dec 89	275	265	540	50.9	67	65.7	607
20 Dec 89	384	385	769	49.9	93	66.7	862
27 Dec 89	362	330	692	52.3	90	61.1	782
3 Jan 90	142	113	255	55.7	80	58.8	335
10 Jan 90	168	138	306	54.9	92	56.5	398
17 Jan 90	271	169	440	61.6	183	57.9	623
24 Jan 90	104	16	120	86.7	42	85.7	162
31 Jan 90	267	14	281	95.0	67	95.5	348
3 Feb 90	89	14	103	86.4	72	94.4	175
10 Feb 90	84	2	86	97.7	45	95.6	131
14 Feb 90	47	4	51	92.2	30	96.7	81
21 Feb 90	11	0	11	100	3	66.7	14
28 Feb 90	2	0	2	100	0	0	2
Totals	3488	2554	6042	57.7	1067	69.3	7109

♂ = ♂ tagged/(♂ tagged + ♀ tagged); Recap % ♂ = % of ♂ recaptures; Total captured = total tagged + recaptures.

Fresh intact but damaged butterflies also were found. Two were found walking around in the litter almost decapitated, damage only in the area between the head and thorax, where the towhee immobilized the prey by biting the butterfly. The heads, occasionally found in the litter, were then lost as the towhee removed the wings.

Predation by towhees occurred in the early morning hours from an hour before until two hours after sunrise (see Table 1). The towhees were observed sallying ("sally-strike") for flying monarchs on two occasions but were unsuccessful. On one occasion, a butterfly was dislodged from the tree and "flutter-chased" unsuccessfully. The sallying behavior occurred when the butterflies were beginning to fly and were quite slow. Predation was never observed during the rest of the daylight hours or during sunset, even though monarchs were seen roosting and flying about.

Table 2 shows the tagging record for 6042 monarchs during the 1989-90 season at this site. The sex ratio is skewed favoring males (57.7%, Chi-square = 72.625, df = 1,  $P < 0.001$ ).

Predation was noticed first on 3 January 1990, rose dramatically thereafter, and remained high until late February when the colony size

TABLE 3. Summary of predated butterflies collected at weekly intervals from the litter at KSP site for 1989-90.

Date	♂	♀	% ♂	?	Total	$\bar{x}$ /day
3 Jan 90	3	3	50.0	0	6	0.9
10 Jan 90	29	27	51.8	2	58	8.3
17 Jan 90	105	69	60.3	4	178	25.4
24 Jan 90	81	58	58.3	7	146	20.9
31 Jan 90	73	27	73.0	2	102	14.6
3 Feb 90	74	56	56.9	0	130	43.6
10 Feb 90	98	46	68.1	2	146	20.9
14 Feb 90	133	47	73.9	1	181	45.2
21 Feb 90	163	66	71.2	2	231	33.0
28 Feb 90	47	14	77.0	1	62	8.9
7 Mar 90	22	9	71.0	1	32	4.6
14 Mar 90	10	6	62.5	0	16	2.3
21 Mar 90	13	1	92.5	0	14	2.0
Totals	851	429	66.5	22	1302	

? = sex undetermined; Total =  $\delta + \varnothing + ?$ ; %  $\delta = \delta / (\delta + \varnothing)$ ;  $\bar{x}$ /day = average number of butterflies eaten per day each week.

declined to a few hundred individuals. Predation ceased by 21 March 1990 when the butterflies left. Table 3 shows the total number and sex ratio of butterflies remains collected at each sampling period. The rate of predation varied from 14.6 to 43.3 butterflies per day for samples from 17 January to 21 February 1990. Earlier samples were omitted as the towhees were learning to exploit the resource, and later samples were omitted as the resource diminished. The average for this period was 22.7 butterflies per day. Since this was the work of a single pair of rufous-sided towhees, each bird was eating an average of 11.4 butterflies/day.

Thirty-eight butterflies were found on 12 January, two days after the previous census, and 38 butterflies were found on 13 January. An average of 19 butterflies was eaten on 10-12 January and 38 butterflies were eaten on 12-13 January.

The total number of dead butterflies collected in the litter was 1302. Taking this colony with a peak population visually estimated at 20,000, this was a 6.51% mortality. A mortality estimate of 7.43% can be derived based on the number of butterflies tagged and the number of butterflies preyed upon by the towhees. These estimates were, however, misleading as the population size was steadily declining (visually estimated at 5000 on 17 January) when predation plateaued. By late February, the towhees were taking most of the remaining butterflies; thus, the 6.51-7.43% annual mortality estimate is extremely conservative.

A Chi-square was calculated comparing the actual sex ratio of the butterflies when the birds were feeding based on Table 2 with the sex ratio of eaten butterflies in Table 3. The Chi-square value of 0.185 (df

TABLE 4. Summary of preyed upon tagged and untagged butterflies collected at weekly intervals from the litter at KSP site for 1989-90.

Date	Untagged				Tagged				?	T
	♂	♀	% ♂	X <sub>u</sub>	♂	♀	% ♂	X <sub>t</sub>		
3 Jan 90	3	3	50.0	6	0	0	0	0	0	6
10 Jan 90	14	21	40.0	35	15	6	71.4	21	2	58
17 Jan 90	76	58	56.7	134	29	11	72.5	40	4	178
24 Jan 90	37	39	48.7	76	44	19	69.8	63	7	146
31 Jan 90	42	23	64.6	65	31	4	88.6	35	2	102
3 Feb 90	39	46	45.9	85	35	10	77.8	45	0	130
10 Feb 90	37	28	56.9	65	61	18	77.2	79	2	146
14 Feb 90	56	39	58.9	95	77	8	90.6	85	1	181
21 Feb 90	74	40	64.9	114	89	26	77.4	115	2	231
28 Feb 90	29	11	72.5	40	18	3	85.7	21	1	62
7 Mar 90	17	5	77.3	22	5	4	55.6	9	1	32
14 Mar 90	7	6	53.8	13	3	0	100	3	0	16
21 Mar 90	12	0	100	12	1	1	50.0	2	0	14
Totals	443	319	58.1	762	408	110	78.8	518	22	1302

% ♂ = ♂/(♂ + ♀); X = ♂ + ♀ (u = untagged and t = tagged); ? = sex undetermined; T = X<sub>u</sub> + X<sub>t</sub> + ?.

= 1,  $P < 0.68$ ) indicates that the birds were not selective based on the butterfly's sex.

The proportion (17.7%) of previously tagged butterflies (recaptured butterflies in Table 2) in the sample of butterflies being tagged (total captured in Table 2) was compared with the proportion (31.3%) of tagged butterflies found in the preyed upon butterflies collected (Table 4). The data strongly suggest that the birds were selecting tagged butterflies (Chi-square = 130.70, df = 1,  $P < 0.001$ ). The data also were separated on a weekly basis and a paired Student's *t*-test was calculated. The data indicate that there was a very high probability that the tags increased the chances of avian mortality at this site ( $t = -3.86$ ,  $n = 9$ ,  $P = 0.0048$ ).

## DISCUSSION

I first noted predation at the colony late in the season in 1988-89. This and the fact that I looked for it regularly beginning on 13 September 1989 and did not notice it until 3 January 1990 suggests that a learning process was involved. Rufous-sided towhees were seen on several occasions earlier in the season, although it is uncertain whether it was the same pair seen throughout the study. But if it was, they were not eating the monarchs. Once they learned to eat monarchs, the resource was exploited as shown in Tables 3 and 4.

Field observations indicate that monarchs are difficult to spot when roosting in trees. But as sunrise approaches, they begin to open their wings and shiver, or after sunrise, they open their wings to bask to warm up to flight temperature. It was at this time that the towhees

began to find and attack the butterflies in the trees. But once the monarchs became warm enough to fly, towhee predation quickly ceased. Rufous-sided towhees belong to a ground feeding and seed eating sub-family of birds (Emberizinae); thus, the lack of success in sallying is expected once the butterflies are capable of flying (Bent 1968).

In Mexico, Brower and Calvert (1985) found that birds preyed selectively upon males either because they had a lower fat content, higher wet weight, and/or a lower cardenolide content. This was not the case in this study, as the birds ate males in the proportion that they were found in the colony. Certainly the fact that the towhees are cueing in on the tagged monarchs affects the data. Since there is a difference between California and Mexican sites relative to the proportion of monarchs that are emetic as well as in their emetic toxicity (Brower & Moffitt 1974, Fink & Brower 1981, Brower & Fink 1985), the same mechanisms working in Mexico may not apply in California. Fink et al. (1983) have data suggesting that rufous-sided towhees in Mexico are not as sensitive to cardenolides, so the lack of prey selectivity by sex is consistent.

Brower and Calvert (1985) estimated a 9.04% annual morality of butterflies killed by birds in one overwintering Mexican colony. Bell and Dayton (1986) reported annual mortality due to chestnut-backed chickadees to range from 0.345–2.21% in California. This study conservatively estimated a 6.51–7.43% annual mortality.

Bell and Dayton (1986) and Brower and Calvert (1985) found that predation intensity was higher on colder days in California and Mexico, respectively. The lowest predation rate during this study was 14.6 butterflies per day during 24–31 January. During this week, an onsite hygrothermograph showed that there were two 36 hour periods when the temperature never fell below 19°C, well above monarch flight temperature of 13°C. There were essentially five days of warm Santa Ana conditions in southern California. The high temperature kept the butterflies constantly agitated making it difficult for the towhees to catch them. On one such morning, butterflies were able to fly at 0400 h when disturbed.

Based on observations of Bell and Dayton (1986) and Calvert et al. (1979), predators leave a characteristic signature on monarch remains. Perches regularly used by the towhees often had the remains (i.e. wings) of five or six butterflies in the litter under them. Brower et al. (1985) found such caches to be associated with small mammal predators in Mexico.

Orioles, grosbeaks, and chickadees feed in the canopy where the clusters are, so body parts and wings simply rain down onto the ground. Calvert et al. (1979) and Fink and Brower (1981) described the different

methods used by orioles and grosbeaks that feed on monarchs. Bell and Dayton (1986) found the chickadees' mode of feeding is similar to that of orioles. As a comparison, yellowjacket predation involves biting off and carrying away the head and abdomen leaving the thorax with the four wings still attached (Leong et al. 1990, Sakai pers. obs.)

The characteristic signature of rufous-sided towhees is a cluster of four wings found in the litter lacking a body. The heads occasionally are found but are difficult to find in the litter. I suspect that the towhee eats the entire body (head, thorax, and abdomen). Occasional heads in the litter are an artifact of the way the towhees kill the butterflies.

Forty dead, intact butterflies were found in the litter during the course of the study. Towhees were observed attacking and picking up butterflies but later dropping and ignoring them. An untested possibility is that these were highly emetic individual butterflies. Mexican and California monarchs are different in their cardenolide biology, which is expected since they feed on different milkweed species. Brower and Moffitt (1974) report California monarchs were 4.6 to 6.5 times more emetic than their Mexican counterparts, and Brower and Fink (1985) report that 49% of California monarchs contain enough cardenolides to make them emetic to birds while only 10% of the Mexican monarchs were considered emetic. Brower and Calvert (1985) suggest that in Mexico birds feed cyclically because they accumulate cardenolides and must periodically desist to purge their bodies of these toxins. Based on these findings, one would expect less avian predation in California compared to Mexico, since California monarchs are both more emetic and have a greater percentage of emetic butterflies.

Towhees may have learned to distinguish between emetic and non-emetic butterflies. Since the cardenolides are concentrated in the wings and exoskeleton, towhees may avoid eating, or learn not to eat, the most toxic ones as orioles do in Mexico. Assuming attacked but uneaten butterflies are the most toxic, the percent of emetic butterflies in this population is only 3.07% (40/1302). This is quite different from the findings of Fink and Brower (1981) and Brower and Fink (1985) of 49% emetic butterflies in California. There are several possibilities. Towhees are able to distinguish the butterflies without killing the monarchs. Towhees may be like grosbeaks and may be relatively insensitive to high doses of cardenolides. It also may be that the percentages of emetic butterflies and/or the degree of emetic strength found by Brower and his co-workers are not consistent throughout California. These questions certainly deserve investigation.

Brower and Calvert (1985) found that grosbeaks and orioles ate more males than females in the Mexican colonies, as females had  $\frac{1}{3}$  more lipid but a higher cardenolide concentration. Brower and Moffitt (1974)



found that in California males are heavier but females had a higher cardenolide concentration, meaning that it would be more advantageous to eat male butterflies. In this study, more males were eaten, but this may have reflected the skewed sex ratio in the colony rather than any selection of one sex over another.

The actual impacts of butterfly tagging have never been addressed. This study indicates that tagged monarchs are at greater risk of predation by rufous-sided towhees in the overwintering colony. It may be that the white tags serve as a flag to attract the birds and the birds learn to cue in on the tags. Tagged monarchs are certainly quite visible in the trees even to the naked eye. On the other hand, tagged wings are also much more visible in the litter. How much these tags serve to attract predators once the butterfly leaves the colony is unknown. Certainly the migratory nature of the monarch would prevent predators from learning to cue in on the tags.

### CONCLUSIONS

A single pair of rufous-sided towhees was found to be an important predator on monarch butterflies at this southern California overwintering colony site, eating as many as 11.4 butterflies per bird per day, representing a 6.51–7.43% annual mortality. The predation rate seemed to be correlated with weather conditions with warmer weather resulting in lower predation rates. Towhees did not select prey by sex but were found to select a higher proportion of tagged monarchs. The characteristic pile of four wings may be used as a signature of rufous-sided towhees for determining them as a specific avian predator.

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## BEHAVIORAL RESPONSE OF MONARCH BUTTERFLIES (NYMPHALIDAE) TO DISTURBANCES IN THEIR HABITAT—A GROUP STARTLE RESPONSE?

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**ABSTRACT.** Monarch butterflies (*Danaus plexippus* L., Nymphalidae) overwintering in fir forests of Mexico's Transvolcanic Belt fall from their perches at once *en masse* in response to "disturbance" by people or other animals that traverse their colonies. Roosting butterflies were stimulated by movement, noise, wind and breath. Their response, as measured by the number falling from perches, indicates that only breath is overwhelmingly effective in initiating the massive roost disintegrations observed. The response is temperature dependent; it begins about 7°C and increases as temperature rises. This group behavior is likely an adaptation to confuse and disorient bird and possibly mouse predators, increase their reaction time thus allowing the escape of the prey. Advantage may accrue to an individual belonging to a group whose size enhances the startle-effect of roost disintegration.

**Additional key words:** *Danaus plexippus*, Mexico, overwintering biology, predation, protean behavior.

Monarch butterflies (*Danaus plexippus* L., Nymphalidae) overwinter in huge aggregations numbering in the millions in the high altitude fir forests of Mexico's Transvolcanic Belt (Calvert & Brower 1986). When people or other animals pass through the colonies, butterflies may drop from their clusters *en masse* sometimes in great numbers. Their collective falling was named "cascading" by K. Brugger, one of the Mexican monarch colony discoverers (Urquhart 1976). The behavior is not a passive event (Brower & Calvert 1985). The butterflies actively use their wings to cast themselves off their perches in a process that during warm weather sometimes appears explosive. The process may involve a few butterflies to hundreds of thousands of butterflies. When the wings are opened in the process of pushing off, the bright orange dorsal surface is suddenly exposed to view. The effect of tens or even hundreds of thousands of butterflies exposing these surfaces at once and falling from their perches is startling and beautiful.

Guards and posted signs at two overwintering colonies open to tourists located within the ejidos (collective farms)—Rosario, near Ocampo, Michoacan, and Macheros, near Donato Guerra in the state of Mexico—admonish the public not to make loud noises while in the colonies. This request is in part an attempt to preserve the spirit of sanctuary within the butterfly colonies. But its main purpose is derived from a commonly held belief among local people that the cascading behavior of the monarch butterfly is a response to noise, such as speech, made by the visitors as they pass through the colony.

Although there is a strong association between the presence of people

and cascading of butterfly clusters, the precise cause(s) of roost disintegration have not been investigated. In this paper I explore several likely causes.

## METHODS

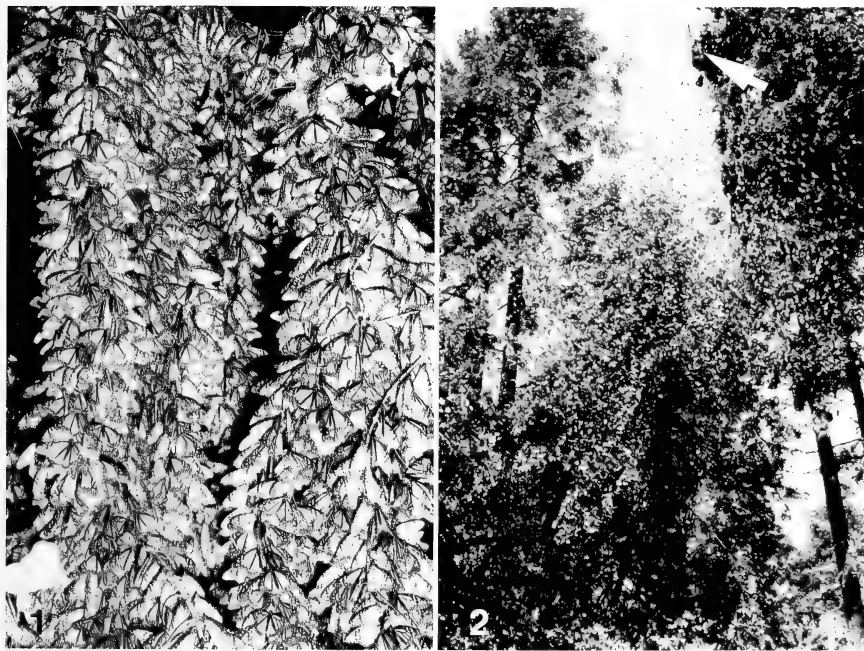
Ten trunk and ten bough clusters ranging in height from 1–2 m and containing several hundred butterflies were artificially “disturbed” by movement, noise, air currents, and human breath. The degree of disturbance was assayed by estimating the number of butterflies cascading out of the roost. The response of roosting butterflies to movement was measured by moving the 2.5 cm diameter  $\times$  20 cm long grey plastic casing of an Omega RH-21C temperature/humidity probe slowly past the clusters approximately 2 cm from the butterflies. The response to loud noise was measured by clapping the hands twice 5–10 cm from the cluster. The hands were clapped together so that air was directed towards the researcher, not towards the butterflies. To test for air movement, the research notebook was waved once back and forth past the cluster rapidly enough so that the wind generated caused a passive movement of the wings. These tests put the researcher and his assistant in close proximity to the butterfly clusters. To avoid the possibility of confounding the tests above with breath, we held our breath and periodically exhaled away from the butterfly cluster. Disturbance from breath was created by the researcher breathing directly on a cluster from a distance of 20 cm. The four types of disturbance were always tested in the order described on each of the ten bough and trunk clusters. The experimentally induced cascading of butterflies had no effect on adjacent clusters as is sometimes observed during warm weather.

The experiment was performed on 29 and 30 January 1988 at the Palomas overwintering colony located on the west face of the Cerro de las Palomas approximately 35 km southwest of Toluca in the state of Mexico (Calvert & Brower 1986). Temperature and humidity of ambient air were recorded by an Omega Engineering, Inc. RH-21C temperature/humidity probe.

## RESULTS

### Disintegration of Roosts or Cascading Behavior

In response to a stimulus, clustered butterflies (Fig. 1) cast themselves off their perches in near synchrony (Fig. 2). This behavior involves more than the opening of the tarsal claws that grip the substrate. Using their wings, they actively push against each other, tree trunks or surrounding foliage. After casting off, they fall *en masse* tumbling over one another, and over foliage and branches until they either gain control



FIGS. 1, 2. 1, Monarch butterflies clustered on a bough of the oyamel fir (*Abies religiosa*). The tightly packed butterflies are oriented in an orderly manner with their wings upright. Original Kodachrome slide by W. H. Calvert. 2, A monarch roost in the process of disintegration. The butterflies are falling in random disarray from a position marked by the white arrow. Original Kodachrome slide by Carlos Gottfried.

and fly or until they strike the ground. The phenomenon gives the impression of a stream of large colored particles pouring downward over branches and foliage (Fig. 2). Cascading in one area of the colony may trigger similar disintegration of roosts in other areas resulting in tens or hundreds of thousands of butterflies leaving their clusters in a half hour period.

An extreme example of cascading behavior occurred on a warm, sunny day in February of 1989 at the Palomas Colony (Calvert & Brower 1986). Cascading began in one cluster at ca. 1400 h. Sequential cascading of clusters throughout the colony continued sporadically for the next hour. By 1500 h a section of forest approximately  $20 \times 30$  m was covered in a living carpet of monarch butterflies ca. 8 cm deep. Excited butterflies were unable to fly but opened and closed their wings, thus pushing and moving against one another giving the appearance of a writhing mat of color. On grades this behavior caused them to flow *en masse* down slope where they piled up against trees or other obstacles such as fallen logs, brush piles or rocks. After several minutes of pushing

themselves about with their wings, unless stimulated by more cascading butterflies falling upon them, they ceased moving their wings and began to crawl. When they encountered vegetation, they crawled upward (Alonso-Mejia et al. 1992).

The majority of cascading events are much less spectacular. Bird predators such as blackheaded grosbeaks (*Pheucticus melanocephalus*) and blackbacked orioles (*Icterus galbula abeillei*) induce butterflies to cascade from positions where they are feeding. Tens to hundreds of butterflies have been observed to fall. More fell during warm ambient temperatures than cold.

Cascading behavior occurs most often when air temperatures are near flight threshold, between 13–15°C (Masters et al. 1988, Kammer 1970) or higher. At high air temperatures (20–25°C), clusters sometimes appear to break up spontaneously and the disintegration of one cluster nearly always triggers the disintegration of others. At air temperatures below flight threshold, multiple disintegrations are rare. Butterflies from a cascading cluster spill onto the ground and flap their wings helplessly. If it is not too late in the day, most of them will crawl up onto foliage (Brower et al. 1977). If air temperatures are above flight threshold or if the butterflies have had an opportunity to bask and have raised their thoracic temperatures to flight threshold (Masters et al. 1988), the falling butterflies will fly before they reach the ground. Sometimes they fly off in the same direction making a striking formation in the air.

### Butterfly Response to Movement, Noise and Wind

The response of clustered butterflies to “disturbances” by movement, noise and wind were measured by counting the number cascading from the roost. There was very little response to the movement of the probe near the clustered butterflies (Table 1). Only on one occasion did a few butterflies fall from a cluster in response to probe movement. This occurred at the relatively high temperature of 9.3°C. There was even less response to a sharp clapping noise. Only one butterfly fell from a cluster (temperature = 4.9°C). More response was evident to the winds generated by the research notebook. Some wing opening occurred at low temperatures of 0.9°C. Movement involving wing opening and small shifts in position occurred at 8.4°C. A few butterflies fell from the roosts at 13°C and higher.

### Butterfly Response to Breath

The major cause of clustered butterflies falling from their perches was breath (Table 1). Butterflies directly in the path of the breath stream cascaded from their perches. A regression of temperature against

TABLE 1. Reaction of clustered overwintering monarch butterflies to movement, noise, air currents and breath.

Time	Exposure	Cluster type	Temp. (°C)	Hum. (%)	Type of disturbance			
					Motion	Sound	Wind	Breath
08:02	Shade	Bough	-0.8	61.1	nc	nc	nc	7+
08:06	Shade	Bough	0.1	63.2	nc	nc	nc	5+
08:09	Shade	Bough	0.1	62.3	nc	nc	nc	4+
08:18	Shade	Trunk	0.9	56.4	nc	nc	1+	2+
08:22	Shade	Trunk	0.9	50.1	nc	nc	1+	3+
10:27	Shade	Trunk	4.9	41.1	nc	1	nc	10
10:31	Shade	Trunk	4.9	43.4	nc	nc	nc	2
10:34	Shade	Bough	5.6	42.0	nc	nc	nc	2
10:38	Sun	Trunk	7.5	37.1	nc	nc	nc	30-40
10:44	Sun	Bough	11.8	34.2	nc	nc	nc	10
13:39	Shade	Trunk	8.9	43.1	nc	nc	nc	40-50
13:43	Shade	Trunk	9.0	42.6	nc	nc	nc	40-50
13:48	Dappled	Trunk	9.3	41.5	3	nc	nc	25-30
13:54	Shade	Trunk	8.3	45.8	nc	nc	nc	15-20
13:58	Shade	Trunk	8.4	43.8	nc	nc	mov't	15-20
14:02	Shade	Bough	8.4	43.2	nc	nc	mov't	40-50
14:06	Shade	Bough	9.0	43.2	nc	nc	nc	~100
14:14	Sun	Bough	13.0	30.4	nc	nc	4	~100
14:18	Sun	Bough	15.0	32.2	nc	nc	3	200-300
14:22	Sun	Bough	15.0	30.3	nc	nc	nc	200-300

nc = no change; mov't = movement without opening wings; + = opened wings but did not drop.

the number of butterflies cascading showed the response to be temperature dependent ( $F = 38.8$ ;  $P = 0.0001$ ;  $r^2 = 0.82$ ). At all but the lowest temperatures, tens to hundreds of butterflies cascaded from their clusters in response to breath. Extremely cold butterflies (air temperature is 1°C or lower) responded to breath by opening their wings without falling from their perch. A few fell from their perches between 4.9°C and 5.6°C. At temperatures between 7.5°C and 9°C, 15 to 100 butterflies fell from their perches. At temperatures greater than 9°C, numbers near a hundred or above fell.

No differences were apparent between cluster types. Bough clustered butterflies were as likely to cascade from their perches as were trunk clustered butterflies. No butterflies left their perches when relative humidity was above 50%, but this is likely an artifact of the inverse relation between temperature and relative humidity ( $r = -0.92$ ) with temperature being the primary determinant of the butterfly response.

## DISCUSSION

These data indicate that neither noise nor movement in the vicinity of clusters caused the cluster disintegration or cascading of butterflies observed during visits to the monarch butterfly colonies. Air currents directed onto clustered butterflies also did not evoke much response.

Some component of breath other than air current appears to be the cause of the massive cascading response. The failure of the butterflies to respond to the close presence of the researcher near the cluster until breathed upon suggests that heat *per se* is not the cause of roost disintegration.

### Erratic Escape Behavior

Cascading behavior of monarchs is clearly more than a simple escape behavior. It involves a rapid, at times explosive, expulsion of numerous animals from a roost nearly simultaneously. The cryptic coloration of the roost suddenly erupts into the vivid orange colors of collective dorsal butterfly surfaces.

Cascading behavior is analogous to behaviors in other animals. Prey animals in many different taxonomic groups behave erratically when attacked by predators (Tinbergen 1951, Roeder 1962, Cott 1940, Marshall & Orr 1955). Such erratic escape behavior, called protean behavior (Chance & Russell 1959), functions as an antipredator device by confusing and disorienting the predator, increasing its reaction time and enhancing the survival of the prey (Humphries & Driver 1967). The erratic and unpredictable nature of the response makes learned countermeasures by the predator less likely (Humphries & Driver 1970).

Cascading behavior is perhaps most analogous to behavior exhibited by certain marine organisms. Antarctic krill maintain synchronized swimming patterns in apparent response to rheotactic cues supplied by the wake of preceding animals (Hamner et al. 1983). When frightened, their synchronized swimming pattern breaks apart, and they disperse in random directions. Monarchs roost in a very orderly manner with their folded wings oriented vertically on boughs or tree trunks (Fig. 1). When disturbed, this oriented assemblage breaks apart; initially the once clustered group tumbles towards the ground (Fig. 2), and if warm enough, flies off in random disarray. If they are able to fly, some sort of orderly flight pattern, likely towards a bright sky, is rapidly obtained.

The elicitation of antipredator responses by mammalian breath may be of general occurrence in some groups of arthropods (Conner et al. 1985). Certain millipeds react to breath by coiling, and they react to a warm surface by emitting defensive secretions. The tenebrionid beetle, *Bolitotherus cornutus*, everts quinone-producing glands when breathed upon. Some component of breath other than CO<sub>2</sub> seems to have elicited the response in the beetle. Possible components eliciting the response in monarchs include heat in the breath or one of the gaseous components of breath such as CO<sub>2</sub> or water vapor. Additional research is needed to determine which breath component evokes this startlingly beautiful defensive behavior in monarchs.



### Microclimate and Bird Predation

Because of their unique position in high altitude tropical forests and presence during the middle of the dry season, the microclimatic regimes of the overwintering colonies are precisely determined by the amount of radiation falling on the area. From the moment solar radiation strikes the area in the morning, parts of the forest begin to heat up and butterflies in the solar path or in the path of diffuse radiation are warmed to flight threshold and empowered to fly. Once solar input ceases in late afternoon, heat accumulated during the day rapidly radiates into the clear, dry sky. Temperatures drop precipitously and the butterflies rapidly lose the ability to respond to stimuli and to escape predators. If temperatures are cold so that the butterflies cannot fly and are forced to remain on the ground or on low foliage until the following day, they are subject to a possibly lethal combination of colder temperatures and higher humidities near the ground (Calvert & Brower 1981, Calvert & Cohen 1983) and to nocturnal mouse predation (Glendinning et al. 1988). If temperatures are warm, or if it is early in the day so that a sun-fleck is likely to strike them, most butterflies will return to their elevated roosts before harm comes to them. However, even when no direct harm comes to them, they must use scarce lipid reserves to crawl up onto foliage or to fly back to their roosts (Masters et al. 1988). Because nectar sources are limited during the overwintering season (Brower & Malcolm 1991), this use of energy reserves could result in premature starvation.

In Mexico's overwintering sites bird, mainly blackheaded grosbeaks (*Pheucticus melanocephalus*) and blackbacked orioles (*Icterus galbula abillei*), and mouse, mainly *Peromyscus melanotis*, predators killed an estimated 926,000 butterflies/ha in a 135 day season (Brower & Calvert 1985, Glendinning et al. 1988) which may have amounted to as much as 10% of the colony population (Calvert et al. 1988). Birds feed during the coldest times of the day usually from dawn to 0900 or 1000 h and from ca. 1630 h till dark (Brower & Calvert 1985). Feeding early and late, birds are likely to encounter cold butterflies unable to move quickly to escape. Birds feeding when solar radiation is striking the colony may encounter butterflies with thoracic temperatures above ambient that are capable of vigorous movement and flight. Attacking while the butterflies are inactivated by the cold would be likely to insure minimum handling cost per effort (Krebs 1978, Brower & Calvert 1985). If the majority of predators are birds which exhale upon clustered monarchs in the process of capturing them, a group startle response such as the cascading behavior designed to confuse and disorient the predator to increase its reaction time would be a beneficial adaptive response to the butterflies.

These data suggest that the butterflies benefiting the most from the cascading response are those whose thoracic temperatures are between ca. 7°C and flight threshold (Table 1). At temperatures lower than this, it is more difficult for them to cast off their perches. At higher temperatures they can fly away to escape predation. Except for the coldest hours of early morning or late evening, most clustered butterflies are likely to experience temperatures in this range. (Exceptions include parts of November and March when ambient temperatures in the forest climb above flight threshold and cold overcast days of winter when ambient temperature never reaches 7°C.) Cascading behavior is unlikely to benefit butterflies being preyed upon by mice since nighttime temperatures when mice feed are nearly always colder than 7°C. The cascading response is most likely to benefit butterflies that are able to cast off of their perches *en masse*, but are unable to fly due to cold air temperatures.

There remains the possibility that two different kinds of cascading phenomena occur in the monarch overwintering colonies. The dramatic disintegration of monarch roosting clusters involving tens of thousands of individuals may be an artifact of gregarious roosting and a different phenomenon from the smaller scale cascading response elicited by avian predators. These multiple cluster disintegrations are especially apparent during warm periods late in the season (February or March) and may be part of the colony breakup in preparation for the return migration to the north. Drawn to nectar and water sources at lower elevations, the colonies rapidly move down slope, often dividing into two or more segments (Calvert & Brower 1986). Mating activity is intensified and each day a portion of the colony leaves to begin its remigration northward (Van Hook 1993).

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## GENERAL NOTES

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### THE CASE OF THE MISSING H: *HELICONIUS CHARITHONIA* (L., 1767), NOT “*HELICONIUS CHARITONIA* (L., 1767)”

**Additional key words:** Nymphalidae, Heliconiini, nomenclature, taxonomy, spelling.

Systematic nomenclature is perhaps the only truly typological part of our science, since it depends on published historical records and not on the vagaries of organismal variation. There are correct names, and there are incorrect names. This little note is about spelling, and thus may seem trivial and pedantic, but there are four reasons why my topic is noteworthy (if you will). First, the taxon in question is the type species of the celebrated genus *Heliconius*, which has enjoyed paradigmatic status in ecological genetics, historical biogeography, and community ecology for several decades. Second, the incorrect spelling of the name is in wide use: a quick scan through literature from the last ten years yields more than a dozen uses of *charitonia* and no uses of *charithonia*. This raises point three: as electronic reference data bases become more prevalent, alternate spellings of names must be eliminated, to promote efficient searching. Lastly, the story behind the confusion is entertaining, if nomenclatorially and historically convoluted.

*Papilio Heliconius charithonia* was described as a species by Linnaeus in the 12th edition of *Systema Naturae* (1767), but, because he considered all butterflies to belong to the genus *Papilio*, the infrgeneric name, *Heliconius* is invalid. (Interestingly, if *Heliconius* L. were valid, the type species would be *H. ricini* L., 1758 and not *H. charithonia*, L. 1767, but that's another story.) For almost 150 years, authors attributed the name *Heliconius* to Latreille (either 1804 or 1805), with a variety of type species including *charitonia* (Fabricius, 1775!).

In 1933, the great historian of lepidopteran systematic literature, Francis Hemming, recognized that *Heliconius* (Latreille, 1804) lacked a valid type species, and selected *charitonia* Fabr., which he equated with *charithonia* L. (Hemming 1933a). Immediately after publication of this designation, Hemming apparently discovered a prior binomial usage of *Heliconius* by Kluk (1802). He quickly published a new designation, this time listing *charitonia* L. as the type species, without the “h” (Hemming 1933b). By 1934, however, Hemming had returned to *charithonia*, and clearly acknowledged the differences in spelling between the early authors, indicating his preference for the Linnaean use of the “h.” This decision is reiterated in his posthumous *magnum opus* (Hemming 1967).

Apparently unaware of Hemming's efforts, Comstock and Brown specifically addressed the problem of the “h” again in 1950. They pointed out that the index of the 12th edition of *Systema Naturae* (1767) makes reference to *charitonia*, as does the 13th edition (1790). They argue further that the name is etymologically derived from *charites*, Latinized from the Greek name for the Graces, and thus logically not containing the “h.” They claimed that since the two spellings are of equal age, and since no other revisers had addressed the issue, they could choose *charitonia* as the proper spelling. Amazingly, in their next paragraph, they coined yet another version of the name, *charitonius*, to produce gender agreement between the genus and the species. This paper appears to be the source of current ubiquitous usage of *charitoni-* (with the -a or -us suffix variously applied).

Five years after Comstock and Brown tried to lay it to rest, the “h” issue rose up yet again in a case submitted to the International Commission on Zoological Nomenclature regarding the priority of names for a crustacean (Holthuis & Hemming 1956). It seems that *Sicyonia thamar*, the name given by Hübner (1816) to what we recognize today as *Heliconius sara* (Fabr. 1793), had priority over a generic name used for a well known genus of prawn (*Sicyonia*, Milne Edwards 1830). Under its plenary powers, the Commission decided to sink *Sicyonia* Hübner, in deference to the request to retain the popular usage of the name for the prawn, and because the butterfly name was not in use, the

species described by Hübner being considered to belong to *Heliconius*. In an addendum to this decision, Hemming, the Secretary of the Commission, officially rejected *Heliconius* Latreille, 1804; *Apostrophia* Hübner, 1816; *Heliconia* Godart, 1819; and *Heliconius* L., 1758. He also placed *Heliconius* Kluk, 1802 on the Official List of Generic Names in Zoology, and, crucial to the point of this note, he put *charithonia* L., 1767 on the Official List of Specific Names in Zoology (Melville & Smith 1987).

Decisions made under the plenary powers of the I.C.Z.N. overrule previous arguments about nomenclature, and thus clearly invalidate Comstock and Brown's (1950) arguments, whether they bear merit or not. It is arguable, however, that Comstock and Brown's views are based on poor interpretations of the International Code of Zoological Nomenclature (Ride et al. 1985). Even if their dubious claim to First Reviser status is valid, giving them the prerogative to choose between alternate spellings in the original description (Article 24(C)), the Code recommends that the spelling that appears first be chosen when it is not obviously wrong or will not fail to serve universality of nomenclature (Recommendation 24(A)). Prior to Comstock and Brown's dictum, most major *Heliconius* systematists (Kirby 1871, Riffarth 1901, Stichel 1906, Eltringham 1916, Seitz 1924, Neustetter 1929, and of course, Hemming 1933a, 1933b, 1934) used *charithonia*. Furthermore, it seems more appropriate to choose the name accompanying the original description than the name listed subsequently in an index, which might have been less subject to editorial scrutiny. Linnaeus' personal copy of the 12th edition of *Systema Naturae* (1767), although filled with hand-written corrections and amendments, shows no suggestion that Linnaeus viewed *charithonia* as a misprint in his text.

With regards to the etymology of the name, there is no extrinsic evidence to suggest that *charithonia* is derived from *Charites*. As Turner (1967) pointed out, many 18th century names do not derive unambiguously from Latin or Greek roots. Turner also chided authors for inappropriate masculinization of specific names to bring them into gender agreement with generic names. Article 31(B(i)) of the Code (Ride et al. 1985) explicitly states that names stand as first published, regardless of gender, unless the author specifically stated that the species name is an adjective modifying the generic name, which Linnaeus did not.

So there we have it. *Heliconius charithonia*, described by Linnaeus (1767), designated as type species of the genus by the rightful First Reviser, Hemming (1933b), and placed on the I.C.Z.N. official list of generic and specific names by Holthuis and Hemming (1956). Yet every major guide to butterflies published since then has followed Comstock and Brown (1950), listing the species as "*charitonia*," (or even "*charitonius*," employing their demonstrably incorrect masculinization). I hope that this minor, yet irritating detail will be corrected in future publications.

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## NATIVE PIERINE BUTTERFLY (PIERIDAE) ADAPTING TO NATURALIZED CRUCIFER?

**Additional key words:** Brassicaceae, diet breadth.

Native butterflies encounter naturalized plants related to their hosts as one consequence of Palearctic weeds spreading throughout North America. Sometimes these plants are incorporated into the butterfly diet and permit a longer flight season (e.g., *Pieris napi microstriata* on watercress: Shapiro 1975; *Papilio zelicaon* on sweet fennel: Sims 1983, Tong & Shapiro 1989, Shapiro in press). In other cases, females do not lay eggs on the naturalized plant so that it is not used, even though it can support complete larval development (e.g., *Colyas philodice* and crown vetch: Karowe 1990). A third alternative

is that females lay eggs on naturalized plants, but larvae die before completing development (e.g., *Pieris napi oleracea*, *P. n. marginata* and *P. virginensis* on garlic mustard: Bowden 1971; *P. n. macdunnoughii* and *P. occidentalis* on pennycress: Chew 1977; *P. napi oleracea* on wintercress: Chew 1981).

Where naturalized plants are attractive to ovipositing females but larvae fail to develop successfully on them, the plants can function as a population sink so that eggs laid on these plants are lost from the population. If appropriate genetic variation exists in the population, selection favors both females that discriminate against the unsuitable plant, and feeding larvae that are able to develop on it successfully (Chew 1977). We report here on a population of *P. napi oleracea* Harris that may be adapting to a biennial weed of Palearctic origin, garlic mustard, *Alliaria petiolata* (Bieb.) Cavara & Grande (Brassicaceae) (nomenclature follows Gleason & Cronquist 1991).

*Pieris virginensis* and *P. napi oleracea* fly together in beech-maple-hemlock woods near Lee and Dalton (Berkshire Co., Massachusetts) and Sandgate (Sandgate Co., Vermont). At Lee, Roger W. Pease, Jr. (RWP) previously observed both species ovipositing on garlic mustard and found eggs and small larvae of *P. n. oleracea* on this plant in July (RWP in litt. and pers. comm.). Rearing these eggs on garlic mustard produced adults with summer brood *P. n. oleracea* phenotypes (RWP pers. comm.). Garlic mustard stands are dense and extensive at this locality and large stands of toothwort, *Cardamine diphylla* (Michx.) A. Wood also are present. Occasional plants of watercress, *Rorippa nasturtium-aquaticum* (L.) Hayek, and cuckoo-flower, *Cardamine pratensis* L., also occur. This site is 17 km from the Dalton site, where both butterflies fly together (Chew 1980) and utilize *C. diphylla*. At Dalton, on 19 August 1993, we observed garlic mustard only in two very small stands near a parking lot; one stand lacked rosettes, indicating that no seeds germinated on this spot during the past spring—a probable indication of recent establishment. To our knowledge, garlic mustard has not been reported previously at the Dalton site. At both sites, toothwort is present above-ground in the spring, but by mid-July its leaves are severely yellowed and unsuitable as *Pieris* food. By contrast, garlic mustard flowering stalks remain green in mid-July, and rosettes remain green throughout the summer.

We confirmed RWP's observations of *P. virginensis* and *P. n. oleracea* females ovipositing on garlic mustard in 1992 and 1993. On 7 May 1993 we collected a single female *P. n. oleracea*. We attempted to rear some of this female's offspring on garlic mustard. Of 34 newly hatched first instar larvae reared on this plant, 14 pupated (8 female, 6 male). Pupal weights for both sexes were not significantly different from weights for sibs reared on hare's-ear mustard. However, larval developmental times (days from egg hatch to pupation) differed significantly for individuals reared on garlic mustard compared to sibs reared on hare's-ear mustard (range on garlic mustard = 16–30 d compared to 14–17 d for hare's-ear mustard; mean  $\pm$  SD for females on garlic mustard =  $23.4 \pm 3.54$  d compared to  $15.5 \pm 1.64$  d on hare's-ear mustard; mean  $\pm$  SD for males on garlic mustard =  $19.0 \pm 2.90$  d compared to  $14.3 \pm 0.58$  d on hare's-ear mustard). All 14 pupae emerged after 6–8 days. Whether these adults were fertile is not known, because they were then placed in a common cage with sibs reared on hare's-ear mustard. The collective cage produced fertile eggs but we cannot be certain whether any came from individuals reared on garlic mustard.

Garlic mustard is a widely used and highly suitable host of *P. napi* and many related species in Europe (Bowden 1971, A. Porter in litt.). But previous attempts to rear North American pierines on garlic mustard have failed, usually in the first or second instar (Bowden 1971; our unpubl. data). F<sub>1</sub> hybrids between North American and English pierines develop successfully on this plant (Bowden 1971). Our only previous success involved 5 *P. n. oleracea* (3 females, 2 males) derived from a combined breeding stock from Lee and central Vermont (near Hancock, Hancock Co., Vermont). These individuals took longer to develop from egg hatch to pupation, but their pupal weights were similar compared to other members of the colony reared on hare's-ear mustard.

Recent work on the behavior of ovipositing *P. n. oleracea* from central Vermont shows that these butterflies are more strongly stimulated by alkenyl glucosinolates such as allyl glucosinolate (sinigrin) than by some other glucosinolates (Chew & Renwick in press). Because allyl glucosinolate is prominent in the glucosinolate profile of garlic mustard

leaves (Chew, F. S., unpubl. data; Renwick, J. A. A., unpubl. data), this plant's attractiveness to ovipositing *P. n. oleracea* is not surprising. Individuals that develop successfully on garlic mustard would be able to use extensive stands of this naturalized host in addition to their toothwort host, and the two hosts together presumably could support a larger butterfly population. Whether the observed variation in larval success on garlic mustard is a remnant of genetic heritage from a pierine ancestral to both North American and European *P. napi* lineages, or whether it is newly arisen in the Berkshire Co., Massachusetts region, is unknown.

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IMPLICATIONS OF INTRODUCED GARLIC MUSTARD  
(*ALLIARIA PETIOLATA*) IN THE HABITAT OF  
*PIERIS VIRGINIENSIS* (PIERIDAE)

**Additional key words:** host expansion, conservation.

*Pieris virginiensis* (W. H. Edwards) (Pieridae) is an uncommon and local univoltine member of the *P. napi* (L.) group from eastern North America, confined to forest understory habitats where its primary hosts, *Dentaria* spp. (Brassicaceae), have relatively dense populations (Opler & Krisek 1984). Most other populations of the *napi* group are multivoltine, as are other *Pieris* species (*brassicae* [L.], *rapae* [L.], *manni* Mayer, etc.). The other univoltine *napi*-group members are confined to habitats with short growing seasons, and typically hybridize in ecotones with multivoltine races (Petersen 1963; my unpubl. data). Allozyme data confirm that *virginiensis* is very close to other North American *napi*-group taxa (Geiger & Shapiro 1992). Univoltinism in *P. virginiensis* is presumed to be a derived adaptation to early senescence of *Dentaria* because summer generations would not have adequate host resources to complete larval growth (Shapiro 1971).

Garlic mustard, *Alliaria petiolata* (M.B.) (Brassicaceae), is an aggressive forest-edge and understory plant that was introduced into northeastern North America from Europe, and has become widespread in the midwestern U.S. since around 1950; there is interest in control of its spread (Willis 1992). *Alliaria* germinates in the spring and summer and forms a large, overwintering rosette, which then bolts in the early spring and blooms from late March to July. Plants with edible foliage can thus be found throughout the year.

At the Cedar Bluffs Nature Preserve in Monroe Co., Indiana, *Dentaria laciniata* Willd. is native and patchily distributed, whereas *Alliaria petiolata* is more widespread on the site. On 1 May 1993, *Dentaria* had already set seed, but the *Alliaria* were still in bloom. At approximately 1400 h, I observed a female *P. virginiensis* while she laid 6 eggs over a 10 minute period. Host-searching behavior was typical for *Pieris*: she flew slowly and frequently contacted leaves and flowers of a variety of plant species, but flew up immediately after contact with non-cruciferous leaves. When she contacted an *Alliaria*, sometimes by diving at the flower (suggesting visual cues were involved), she began searching and alighting on the lower leaves, ~1-2 dm above the ground. In most cases, she would lay a single egg on the underside of a leaf at this height, but several plants were rejected. After oviposition, she always flew at least several meters before searching for the next host. She did not contact any *Dentaria* during this time. After collecting this female as a voucher (retained in my personal collection), I searched *Dentaria*, and occasional *Arabis* (Brassicaceae) plants for 10 minutes, and did not find any eggs or larvae. The female subsequently laid eggs on *Alliaria* in captivity; these eggs were reared into the second instar with moderate mortality before fieldwork overseas terminated the study.

There are three possible outcomes of the use of *Alliaria* as an oviposition site by *P. virginiensis*, and they depend on the palatability of the plant to the larvae. If the plant is toxic, then there are two possible outcomes: the *virginiensis* populations will decline because females waste eggs on *Alliaria*; and/or there will be selection on females to avoid *Alliaria* together. However, if *Alliaria* is palatable, even to some larvae in the population, then *virginiensis* will probably evolve a broader host range because *Alliaria* is a more widespread and reliable resource than *Dentaria*.

Isolated populations of *virginiensis* are likely to be in danger of extinction if *Alliaria* is toxic to the larvae. *Pieris virginiensis* maintains relatively small and localized populations, and does not often fly outside the forest understory. *Alliaria* is likely to be much more apparent than *Dentaria* in *virginiensis* habitat, both because *Alliaria* reaches high abundance over larger areas than *Dentaria*, and because *Alliaria* have larger plants with a longer flowering season. Female *virginiensis* searching for crucifers are likely to encounter and oviposit on *Alliaria* more often than *Dentaria*, and perhaps be prone to fly

out of *Dentaria* patches while continuing to discover *Alliaria* plants. The resulting decline is likely to lead to extinctions of already small *virginiensis* populations before the ability to discriminate can evolve. Even if the ability to discriminate does evolve locally, it is unlikely to spread rapidly and "rescue" other populations because of the philopatric tendencies of *virginiensis*.

On the other hand, it would be a welcome development if *P. virginiensis* were to expand its host range to include *Alliaria*. It would give *P. virginiensis* a better foothold where it does live, and perhaps allow it to expand its range of suitable habitats. In Europe, *Alliaria petiolata* is a common host of *Pieris napi* (Petersen 1963, Bowden 1971; my unpubl. data), but in North America, *P. napi oleracea* Harris has reportedly been unsuccessful on *Alliaria* (Bowden 1971), although I have frequently found *P. rapae* to use it (unpubl. data). Incipient host-range expansion is also of interest to population and community ecologists: because *Alliaria* foliage can be found in abundance throughout the year, natural selection would favor the return of *Pieris virginiensis* to its ancestral, multivoltine life cycle.

Population studies following the historical progress of the interactions between *Alliaria* and *P. virginiensis*, regardless of the outcome, would be quite relevant to our understanding of how host selection and host use evolves in natural populations. For example, *Rhagoletis pomonella* (Diptera: Tephritidae) is presumed to have switched from hawthorn to apple in New York State, whereupon the apple-feeding race spread over the northeastern U.S. (Bush 1968). Even though this case is among the best studied, the evidence for this scenario is weak because historical data are scant, and the switch may as easily have occurred more or less simultaneously in several parts of the species' range. Courant et al. (1994) independently report interactions between *Alliaria* and *P. napi oleracea* and *Alliaria* and *P. virginiensis* in New England, with similar observations to mine from Indiana; notably, New England populations have been in the presence of *Alliaria* longer than midwestern populations and may have had an evolutionary "head start." Strong selection by *Alliaria* is probably occurring over much of the range of *virginiensis*, and simultaneous observations of the interactions in geographically separated populations are needed to help understand processes involved in the evolutionary response to this selection.

This note has benefitted from discussions with Francie Chew and Art Shapiro, and two anonymous reviewers' comments. Francie was kind enough to send me her unpublished manuscript. Thanks are due to Mark Dybdahl and Lynda Delph for accommodations in Bloomington, and to Lynda for identifying the *Dentaria*.

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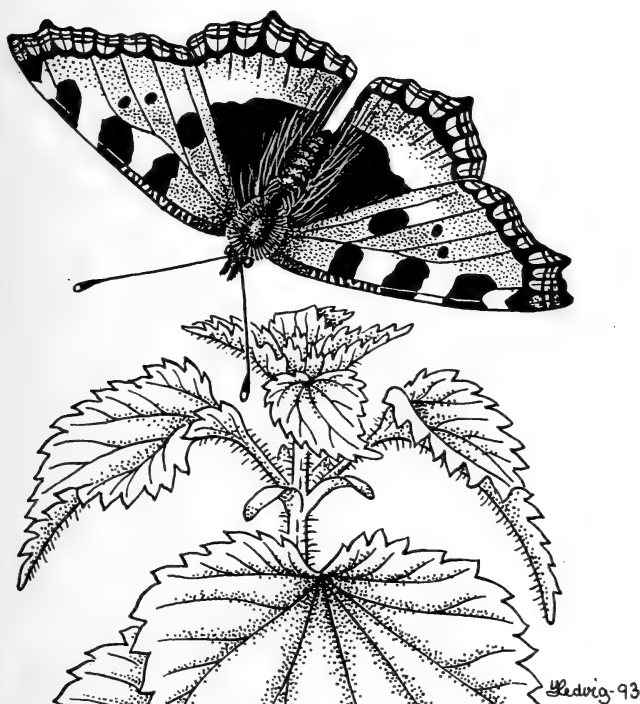
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**Cover illustration:** The European tortoise-shell butterfly, *Aglais urticae*, flying over nettle, *Urtica dioica*. Original drawing by Hedvig Wright Østern, Torsarudstuppen 25, 3430 Spikkestad, Norway.

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## NECTAR SOURCE DIVERSITY AS AN INDICATOR OF HABITAT SUITABILITY FOR THE ENDANGERED UNCOMPAHGRE FRITILLARY, *BOLORIA ACROCNEMA* (NYMPHALIDAE)

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**ABSTRACT.** Pairwise comparisons between occupied and apparently suitable, yet unoccupied, *Boloria acrocneuma* sites in the San Juan Mountains of southern Colorado indicated that occupied sites have a greater diversity of nectar source genera than unoccupied sites. This suggests a means of improving the efficiency of search efforts for additional populations of this endangered butterfly.

**Additional key words:** habitat, Colorado, conservation, biological indicators.

The Uncompahgre fritillary, *Boloria acrocneuma* (Gall and Sperling) (Nymphalidae), was discovered on a high ridge near Uncompahgre Peak in the San Juan Mountains, Hinsdale County, Colorado in 1978 (Gall & Sperling 1980). A second colony subsequently was found in 1982 near Red Cloud Peak, approximately 16 km south of the type locality (Gall 1984a). Despite considerable effort throughout the 1980's, U.S. Fish and Wildlife Service, Forest Service, and Bureau of Land Management personnel and others were unable to document the existence of any additional colonies. Gall (1984b) estimated the total brood size of the Uncompahgre Peak colony at 650-750 individuals in 1980. The Red Cloud colony consisted of 1,000-1,500 individuals in 1982 (Gall 1984b). Anecdotal accounts indicated that both known colonies were declining.

Given the extreme endemism of this butterfly and its apparent rarity, the species was considered for endangered status under the U.S. Endangered Species Act in 1982 (Federal Register, Vol. 49, No. 100, P. 2167). Work was begun in 1987 to characterize the habitat of the Uncompahgre fritillary, determine the status of the known populations,

and discover any existing colonies near the known ones (Britten & Brussard 1992, Britten et al. 1994). Because the populations were declining, and because the odd-year brood of this biennial butterfly was apparently extirpated at its type locality in 1987 (Britten et al. 1994), the Uncompahgre fritillary was listed as endangered in 1991 (Federal Register, Vol. 56, No. 121, P. 28712).

The 1993 draft recovery plan for the Uncompahgre fritillary stipulates that delisting of the butterfly will occur when stable colonies exist for 10 consecutive years at 10 or more locations. Because only small numbers ( $n < 15$ ) of butterflies were located at three additional sites (Brussard & Britten 1989), delisting will occur only with the discovery of a substantial number of new colonies. However, the search for colonies is hampered by a number of difficulties. First, the known colonies exist at high elevations, approximately 4,000 m, in areas which generally are inaccessible by road. Thus, foot travel or high altitude helicopters are the only realistic means of access to potential habitat areas. Second, this butterfly's flight season is short, lasting from early- to mid-July to early August. In addition, weather conditions are unpredictable at high elevations. This diminishes further the duration of suitable flight conditions in which searches can be conducted. As poor flight conditions frequently occur during investigations, it is often impossible to eliminate a site as potential habitat. The final difficulty in locating new colonies is that apparently suitable habitat is ubiquitous in the San Juan Mountains and nearby ranges.

Larval *B. acrocnema* feed on snow willow, *Salix nivalis* (Booth) (Salicaceae) (Scott 1986), which occurs in fairly discrete patches from below tree-line to near the limit of vegetative growth in the San Juan Mountains. The two known colonies and other areas where the butterfly has been located, have approximately 15% snow willow cover, occur on northeast facing slopes with up to 45% grades, and contain snow fields and numerous flowers during the flight season (Brussard & Britten 1989). These characteristics describe a very large portion of the alpine zone of the southern Rocky Mountains. All sites examined have similar habitat components, yet only a small fraction of them support *B. acrocnema* populations. Thus, an efficient method of habitat assessment is much needed.

A number of studies have correlated adult butterfly resources, such as nectar supply, with population densities and individual movements (Gilbert & Singer 1975, Thomas & Singer 1987, Williams 1988). We examined data on nectar source inflorescences to test for a similar correlation between occupancy at potential *B. acrocnema* sites and nectar source abundance. Any such quantifiable differences between



occupied and unoccupied sites could then be used to establish search priorities among sites for this rare butterfly.

#### MATERIALS AND METHODS

Data were gathered during the 1988 flight season from the five occupied sites and from five unoccupied sites which were paired to the former on the basis of elevation, slope, aspect, geographical location, and percent cover of snow willow. Unoccupied sites were no more than 200 m from the occupied sites with which they were paired. The unoccupied sites originally had been identified as good potential sites, due mostly to the presence of a patch of snow willow, and were surveyed for butterflies, along with a total of approximately 50 such sites, in the initial efforts to locate new colonies. The unoccupied sites were selected for comparison with the occupied sites because of their proximity to the latter. Nearness of paired sites is desirable for these comparisons, because it insures that unoccupied sites are as ecologically similar to the occupied sites as possible.

Data on frequency of nectar source inflorescences by genus were determined using a line intercept method along habitat transects (Smith 1980). This was accomplished by laying a 50 m tape measure across the potential habitat patch and tallying all flowering plants which came into contact with the tape measure (Britten 1991). Flowering plants are referred to as "nectar sources" if *B. acrocnema* was observed visiting the species during the flight season (Britten 1991). Transect length varied from 75 m to 150 m according to the length of the site, but the majority of sites were sampled with 100-m transects. Size of a site was not correlated with occupancy. Sites were characterized by frequency of inflorescences by genus (occurrence per meter) and the number of genera represented.

The hypothesis that occupied sites are floristically more diverse than unoccupied sites was tested against a null hypothesis that unoccupied sites are equally or more floristically diverse than occupied sites. Thus, one-tailed statistical tests were appropriate for the rejection of the null hypothesis.

The diversity of nectar source genera was compared among paired sites using  $N$ , the number of genera per site, and  $1/D$ , the reciprocal of the Berger-Parker index of dominance (Magurran 1988). The Berger-Parker index indicates how dominant the most common taxon is within a site. Its reciprocal, therefore, gives an estimation of evenness. Taken together, taxon richness ( $N$ ) and evenness ( $1/D$ ) estimate site diversity. These data may not be normally distributed, and, thus, they require nonparametric analysis. The Wilcoxon signed ranks test was used to

TABLE 1. Inflorescences present (+) or absent (-) on paired occupied (O) and unoccupied (U) *Boloria acrocnema* sites in the San Juan Mountains.

Genus	Sites									
	Uncompahgre		Red Cloud		A		B		C	
	O	U	O	U	O	U	O	U	O	U
<i>Aster</i> (Asteraceae)	+	+	-	+	+	-	+	+	+	+
<i>Bistorta</i> (Polygonaceae)	-	+	-	-	-	-	-	-	+	+
<i>Caltha</i> (Ranunculaceae)	-	-	-	-	-	+	-	-	-	-
<i>Castilleja</i> (Scrophulariaceae)	+	+	+	+	+	-	+	+	+	+
<i>Draba</i> (Cruciferae)	-	-	+	-	-	-	-	-	-	-
<i>Dryas</i> (Rosaceae)	-	-	-	-	-	-	+	-	-	-
<i>Hymenoxys</i> (Asteraceae)	+	-	-	-	-	-	-	-	-	-
<i>Lomatium</i> (Umbelliferae)	-	-	+	-	-	-	-	-	-	-
<i>Mertensia</i> (Boraginaceae)	+	-	-	-	-	-	-	-	-	-
<i>Penstemon</i> (Scrophulariaceae)	-	-	-	-	-	+	-	-	-	-
<i>Phlox</i> (Polemoniaceae)	+	-	-	-	-	-	+	+	-	-
<i>Polygonum</i> (Polygonaceae)	+	-	+	+	-	-	+	-	-	-
<i>Potentilla</i> (Rosaceae)	+	+	+	+	+	+	+	+	+	-
<i>Silene</i> (Caryophyllaceae)	-	-	+	+	+	+	+	-	-	-
<i>Trifolium</i> (Fabaceae)	+	-	+	-	-	-	+	-	+	-
<i>Zigadenus</i> (Liliaceae)	-	-	+	-	-	-	-	-	-	-

compare N and 1/D between occupied and unoccupied sites. Paired sites were further compared using the frequencies of all flowers encountered per meter of transect and the frequency of *Potentilla* (Rosaceae) species encountered per meter of transect. *Potentilla* was chosen for this analysis because it was by far the most abundant flower on the study sites. These final between-site comparisons were made with a t-test, as nonparametric tests were not required (Sokal & Rohlf 1981).

## RESULTS

The results of the analyses demonstrate that occupied *B. acrocnema* colony sites are more floristically diverse than nearby unoccupied sites. Flowers present at each site are indicated in Table 1. The number of

TABLE 2. Comparison of nectar source diversity for paired occupied and unoccupied *Boloria acrocneuma* colony sites. N is the number of nectar source genera represented on each site and 1/D is the reciprocal of the Berger-Parker index of dominance (Magurran 1988).

Paired sites	N		1/D	
	Occupied	Unoccupied	Occupied	Unoccupied
Uncompahgre*	8	4	3.00	2.09
Red Cloud	8	5	1.70	1.77
A	4	4	1.65	1.50
B	8	4	3.10	1.20
C	5	3	3.20	1.30
P = 0.03		P = 0.04		
1-tailed Wilcoxon signed ranks tests				

\* Type locality.

genera in flower per site, N, was higher at occupied than unoccupied sites ( $P=0.03$ ; Table 2). The reciprocal of the Berger-Parker index, 1/D, was higher at occupied sites ( $P=0.04$ ; Table 2). The number of flowers encountered per meter was higher at occupied sites ( $P=0.04$ ; Table 3). This may be, in part, because of the dominance of *Potentilla* species at most sites. The frequency of *Potentilla* species was higher at occupied sites ( $P=0.03$ ; Table 3). Finally, *Trifolium* species (Fabaceae) occurred at four out of the five occupied sites, but at none of the unoccupied sites (Table 4).

## DISCUSSION

The results of the present study are similar to those of Williams (1988) for the montane checkerspot *Euphydryas gillettii* (Barnes) (Nymphalidae) in the Rocky Mountains. Williams (1988) quantified 10 habitat variables including topographic characteristics, larval host abundances, and nectar source abundances at 15 *E. gillettii* sites in Wyoming,

TABLE 3. Comparison of flower density among paired occupied and unoccupied *Boloria acrocneuma* sites.

Paired sites	Flowers/meters		<i>Potentilla</i> /meter	
	Occupied	Unoccupied	Occupied	Unoccupied
Uncompahgre*	0.16	0.15	0.05	0.07
Red Cloud	0.57	0.19	0.33	0.10
A	1.19	0.12	0.72	0.08
B	1.67	0.20	0.46	0.16
C	0.73	0.47	0.23	0.00
P = 0.04		P = 0.03		
1-tailed <i>t</i> -tests				

\* Type locality.

TABLE 4. Presence (+) or absence (-) of *Trifolium* species in flower at paired occupied and unoccupied *Boloria acrocneuma* sites.

Paired sites	Occupied	Unoccupied
Uncompahgre	+	-
Red Cloud	+	-
A	-	-
B	+	-
C	+	-

Montana, Idaho, and Alberta. Nectar source abundance was the only variable that significantly correlated with *E. gillettii* colony size (Williams 1988). Likewise, the higher floristic diversity of occupied *B. acrocneuma* sites relative to nearby unoccupied sites is probably the result of ecological correlations rather than direct causal mechanisms, such as relative nectar source availability. In other words, habitat characteristics which make a site more suitable to flowering plants also may do the same for *B. acrocneuma*. Therefore, it is possible that some as yet unknown set of habitat variables determine habitat suitability for *B. acrocneuma* and that the frequency of inflorescences is an ecological indicator of these favorable habitat sites.

The search efforts of federal personnel up to this point have relied on three criteria for the identification of potential *B. acrocneuma* colony sites: 1) the presence of snow willow, 2) northeastern aspects, and 3) approximate elevations greater than 3500 m. The results of the present study suggest that it would be prudent to include some assessment of flower frequency in the evaluation of potential habitat. This perhaps could be accomplished with a technique as simple as estimating the density of flowering *Potentilla* plants and noting the presence of *Trifolium* on all investigated sites.

High quality *Boloria acrocneuma* habitat seems to be characterized by quantifiable parameters with respect to nectar source inflorescences. These habitat measures should not replace population studies, but they may be used to expand search efforts temporally. Thus, whereas current search efforts are possible only during the three week flight season, habitat assessment including nectar source evaluation could occur throughout the summer. Such inventories could be used to locate new colonies and prioritize sites for further monitoring during the flight season.

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HIGH ANDEAN PRONOPHILINI FROM VENEZUELA:  
TWO NEW SPECIES OF *DIAPHANOS*  
(NYMPHALIDAE: SATYRINAE)

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**Abstract.** *Diaphanos fuscus*, new species, and *D. curvignathos*, new species, are described and illustrated from the Cendé and Niquitao areas, respectively, in the States of Lara and Trujillo in the Andes of Venezuela. The two new species are compared with the type-species of the genus, *D. huberi*, which is known from the Cordillera de Mérida. A key for separating the three species is presented. Comments on the biology, habitat, and distribution of the new taxa are presented.

**Additional key words:** *Diaphanos fuscus*, *D. curvignathos*, *D. huberi*, endemic species, páramo.

The montane butterfly fauna of northern South America is exceptionally diverse, especially the Satyrinae, which contains many endemic elements. Within the subfamily, the genera *Paramo*, *Dangond*, *Redonda*, and *Diaphanos* are considered "relicts" (Adams & Bernard 1981, Adams 1985); they are restricted to high altitudes in the isolated páramos of the Sierra Nevada de Santa Marta (Colombia), Sierra de Perijá (Colombia-Venezuela), and Cordillera de Mérida in Venezuela.

Adams and Bernard (1981) described the genera *Redonda* and *Diaphanos* from the highlands of the Mérida range, believing both to be monobasic. *Diaphanos huberi* Adams and Bernard is the most unusual satyrid of the tribe Pronophilini because of its small size, coloration (almost transparent), and other peculiar morphological features.

During an inspection of the butterfly collection at the Museo del Instituto de Zoología Agrícola of the Universidad Central de Venezuela, I found a single worn male of a dark *Diaphanos* from Páramo del Jabón, Lara State, which was distinct from *D. huberi*. This led me to visit Fila de Los Nepes (near Páramo del Jabón) in August 1991, where I observed the butterfly in its natural habitat and collected additional specimens. Subsequently, J. Camacho of the Universidad del Zulia (MALUZ) showed me similar specimens from Páramo de Las Rosas, south of Los Nepes and nearer El Jabón, a place where this species is locally common. It became apparent that all these specimens represented an undescribed taxon. I was interested in establishing the western distributional limit of this new *Diaphanos*, and during additional field work, I collected the genus in the Páramo de Ortiz, Trujillo State. The latter specimens are smaller in size and lighter in color. The genitalia are distinct, indicating that the specimens from Trujillo represent an additional undescribed species. In this paper I describe these two new

species and present life history observations. A key to the species based on wing coloration and distribution also is presented.

**Disposition of material.** The holotypes and most of the paratypes are deposited in the Museo de Artrópodos de la Facultad de Agronomía of La Universidad del Zulia (MALUZ) and in the Museo de Biología de La Universidad del Zulia (MBLUZ), both in Maracaibo, Venezuela. Representative paratypes are deposited in the Museo del Instituto de Zoología Agrícola de la Universidad Central de Venezuela, Maracay (MIZA); The Natural History Museum, London, England (BMNH); and the private collection of Tomasz Pyrcz, Warsaw, Poland (TPP).

## SYSTEMATICS

### Key to the Species of *Diaphanos* in the Venezuelan Andes

1. Wings translucent, Mérida range ..... *D. huberi*  
    Wings not translucent; dorsally fuscous or dark brown ..... 2
2. Hindwing underside with one cream-white streak in cell  $A_2$  (Cendé range) .....  
    ..... *D. fuscus*, n. sp.  
    Hindwing underside with two cream-white streaks in cell  $A_2$  (Niquitao range) .....  
    ..... *D. curvignathos*, n. sp.

### *Diaphanos fuscus* Viloría, new species

(Figs. 1, 2, 4, 6)

**Description.** Eyes glabrous, dark brown, circled with reddish brown. Palpus twice as long as head, chestnut brown with dark fuscous hairs. Antenna to 0.40 length of costa; shaft orange-brown, sparsely scaled; club black, tapered (not as blunt as in *D. huberi*), 2.5 to 3.0 times longer than broad, concave, comprising eleven segments. Wing venation as in *D. huberi*. Forewing tornus obtuse. Both wings rounded; dorsal surface covered with spindlelike scales that are dentate distally, broader distally (triangular shaped) in females. Marginal scales spinelike, each dentate at distal extreme; scales longer in female (Fig. 6).

**Male.** Forewing length 17–21 mm ( $n = 23$ ) (Fig. 1). Body dark fuscous, tip of abdomen lighter. Upperside ground color of wings dark fuscous, glossy, slightly lighter towards outer margins. Dorsal surface of wings hairy; hairs longer and more abundant in basal half, especially on hindwings. Underside ground color as on upperside, but lighter and more opaque. Hindwing underside with spindlelike cream-white streak parallel to veins, extending through discal cell and  $M_3$  from base to near outer margin, interrupted by  $M_2$ – $M_3$ ; a series of narrow cream-white streaks parallel to the veins, from near discal cell to near outer margin, in cells  $Cu_1$ ,  $Cu_2$ , and  $A_2$ . Ventral surface of wing densely hairy. Genitalia as in Fig. 4.

**Female.** Forewing length 16–19 mm ( $n = 8$ ) (Fig. 2). Dorsal surface of body dark fuscous, ventral surface brown. Wings slightly narrower and forewing apex sharper than in male. Scales and hairs on both wing surfaces less dense than in male. Upperside ground color fuscous, darker at base, dusted with brown scales mainly in distal half of both wings. Underside ground color light brown, with golden sheen, dusted throughout with fuscous scales, more dense in basal one-third of both wings. Forewing underside with series of narrow and vestigial white streaks parallel to veins, from discal area to outer margin, in cells  $M_1$  to  $Cu_2$ ; cell  $A_2$  dusted with white scales near tornus. Hindwing underside with series of white streaks as in male, but less distinct.

**Variation.** Wing maculation is variable in males. In a few specimens the forewing upperside is dusted with gray scales in the discal and postdiscal areas. The ground of





both the upper and underside may be olivaceous or brownish. In some individuals the distal one-fourth of the fore- and hindwing undersides have a chestnut tone. All streaks on the hindwing underside are highly variable. They may reach the outer margin or not; sometimes only vestigial streaks are present (except for the longer spindlelike one which is always well defined). The most strikingly marked individuals have an additional streak in cell  $M_2$  and a speckling of cream-white scales near the streak in  $A_2$ .

Variation among females is apparent on the underside of the wings where the ground color may be as light as cream-white. In this case it is difficult to distinguish the white streaks on both wings, except for the longer spindlelike streak of the hindwing. The most heavily marked individuals have additional narrow streaks in cell  $M_2$  and  $A_3$ .

**Types.** Holotype: male, Fila de Los Nepes, Páramo de Los Nepes, 2550 m, Lara State, Venezuela (9°45'N, 70°04'W), 12 Aug. 1991, A. Viloría & J. Camacho (MALUZ). Paratypes: 22 males, 8 females as follows: VENEZUELA: Lara State: 3 males, 4 females, same data as holotype (MALUZ); 1 male, Páramo del Jabón (9°30'N, 70°06'W), 3000 m, 20 Feb. 1985, CEUM (MIZA); 18 males, 4 females, Páramo de Las Rosas, Municipio Morán (9°36'N, 70°07'W), 3150 m, 20 Aug. 1991, J. Camacho (MIZA, BMNH, TPP, MALUZ).

**Etymology.** The name *fuscus* refers to the dark coloration of this species.

**Comments on the Natural History.** *Diaphanos fuscus* is locally common in the páramos of Los Nepes, Las Rosas, and El Jabón, all of which belong to the massif of El Cendé (Fig. 7). El Cendé is considered one of the most isolated páramo units of the Venezuelan Andes (Simpson 1971, Vuilleumier 1979). The species probably is restricted to this páramo unit which includes the states of Lara and Trujillo.

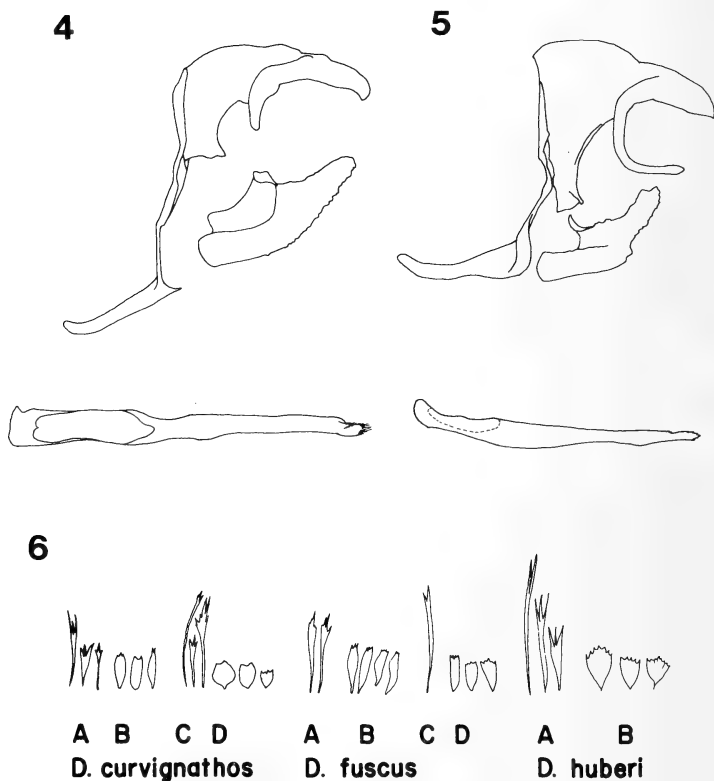
Northeastern slopes of the Cendé range (the Los Nepes area) are relatively arid; consequently, the páramo vegetation—with characteristic speletine composites—is developed from 2400 m, although there are some forest patches near La Fila (2500 m). *Diaphanos fuscus* flies only in páramo habitat and has been collected from 2550 to 3150 m.

During a visit to Los Nepes in August 1991, the weather was mostly windy and foggy. No butterflies were seen until the clouds cleared between 1140 and 1330 h. All individuals observed and collected were from a small open area surrounded by low shrubs (1.5 m tall) of *Libanothamnus* (Asteraceae). The butterflies flew weakly, close to the grasses and over the shrubs, and never more than 2 m above the ground.

A single female was observed resting and displaying on the flowering spike of a "palmiche" (*Orthosanthus chimboracensis* Bak., Iridaceae) in a supposed thermoregulatory posture exhibited by other páramo butterflies (Descimon 1986, Viloría unpublished). Two other females

←

FIGS. 1–3. Upperside (left) and underside (right) of *Diaphanos* species. 1, *D. fuscus*, n. sp., female, same data as holotype; 2, *D. fuscus*, n. sp., holotype, male, Fila de Los Nepes, Páramo de Los Nepes, Lara State, Venezuela; 3, *D. curvignathos*, n. sp., holotype, male, Páramos de Ortiz, Trujillo State, Venezuela.



FIGS. 4-6. Male genitalia and wing scales of *Diaphanos* species. 4, Male genitalia of *D. fuscus*; 5, Male genitalia of *D. curvignathos*; 6A, Marginal scales in male; 6B, Dominant scales on wing surface of males; 6C, Marginal scales in females; 6D, Dominant scales on wing surface of females.

flew from some palmiches when these plants were disturbed. Three females from Los Nepes remained alive for at least 30 hours following their capture. Each oviposited 4 to 15 eggs inside paper envelopes without attaching them to any surface. The most prolific female died still containing many eggs in its abdomen.

The egg (Fig. 8) is spherical (1.0 mm in diameter), pale green, smooth, and free of cement or glue. Examples are deposited in MBLUZ.

It is interesting that some females of *Redonda* from Páramo de Ortiz (Trujillo) had a similar but more violent oviposition behavior, releasing large numbers of eggs into paper envelopes immediately after their capture (Viloria personal observation). This may be an instinctive response to the stress of capture and handling. It also suggests that these butterflies may not place their eggs directly on the host, but may

broadcast them. Non-plant oviposition substrates have been reported previously for butterflies by Chew and Robbins (1984). In addition, DeVries (1987) reported that some Neotropical satyrid species expel their eggs while flying, so that eggs are dispersed over the plants or among the grasses on the ground, and this may be the case in *D. fuscus*.

As for all Pronophilini, it is believed that a bambusoid grass is the host plant of *Diaphanos fuscus*. In my experience, bamboos are scarce in Los Nepes (but much more common in Las Rosas), and they grow mainly in the herbaceous strata under *Libanothamnus* shrubs. The only bamboo species recorded from Los Nepes is *Rhipidocladum geminatum* (McClure) (Clark & Londoño 1991), but other species occur within the Cendé massif [e.g., Clarke (1989) reported *Chusquea angustifolia* (Soderstrom & C. Calderón) in Las Rosas]. Other dominant plant species in the highlands of Cendé are the grasses *Agrostis* and *Calamagrostis* (Poaceae) and the composites *Espeletia*, *Espeletiopsis*, *Ruilopezia*, and *Hinterhubera* (Asteraceae) (Vareschi 1970, Cuatrecasas 1979). The only pronophiline butterfly recorded in association with *D. fuscus* is an undescribed species of *Redonda* (Viloria & Pyrcz unpublished).

### *Diaphanos curvignathos* Viloria, new species

(Figs. 3, 5, 6)

**Description.** Eyes glabrous, dark brown. Palpus twice as long as head, light brown, with fuscous and chestnut hairs. Antenna to 0.4 length of costa; shaft orange-brown, almost without scales; club black, slightly more gradual than in *D. fuscus*, three times longer than broad, concave, comprising eleven segments. Venation similar to other species of *Diaphanos*. Forewing tornus obtuse; both wings rounded. Most of dorsal surface covered with suboval scales, longer on hindwing, broader and rounded in females. Some lighter, spindle-like scales, like those of *D. fuscus* male, dusted over entire wing surface. Marginal scales spinelike, dentate distally; longer in female (Fig. 6).

**Male.** Forewing length 14–17 mm ( $n = 11$ ) (Fig. 3). Body dark fuscous, slightly lighter on distal and ventral regions of abdomen. Upperside ground color of wings dark brown, glossy, lighter and reddish from distal region to outer margins. Dorsal surface of wings hairy; hairs longer and most abundant in basal one-half and anal region, especially long on hindwing. Basal one-half of forewing underside fuscous, becoming light brown in distal one-half. Hindwing underside light brown, becoming fuscous towards base and center of wing. Discal cell almost entirely cream-white; a series of narrow cream-white streaks parallel to veins, from discal cell to outer margin, in cells  $M_2$  to  $A_2$  (two streaks in latter). Ventral surface of wings densely hairy. Genitalia as in Fig. 5.

**Female.** Forewing length 16 mm ( $n = 1$ ). Essentially as described for male.

**Variation.** Variation among the specimens studied is slight. In some males the upperside ground color of the distal two-thirds of the wings is ochereous rather than reddish, and the cream-white scales in the discal area and streaks on the hindwing underside are pale yellow. In darker individuals, the streaks are reduced but still distinct. In lighter individuals, there are cream-white scales in the costal region of the hindwing underside.

**Types.** Holotype: male, Páramo de Ortiz, 2850–3100 m, Trujillo State, Venezuela (9°13'N, 70°24'W), 12 Sept. 1991, A. Viloria & E. Moscó (MBLUZ). Paratypes: 10 males, 1 female as follows: VENEZUELA: Trujillo State: 5 males, same data as holotype (BMNH, MBLUZ, TPP); 5 males, 1 female, Paramo de Ortiz, 2900–3000 m, 7 Jan. 1992, A. Viloria & J. Camacho (MALUZ).

**Etymology.** The specific epithet *curvignathos* is a composite of the Latin *curvus* (=

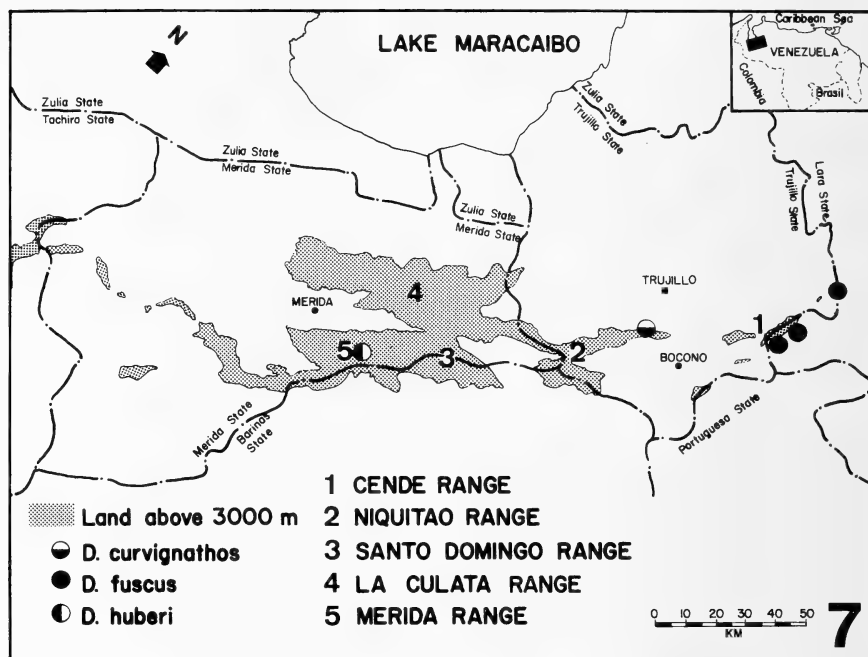


FIG. 7. Geographical distribution of the Venezuelan highlands and distribution of the three species of *Diaphanos*.

curved) and the Greek *gnathos* (= mandible, also the name of the subuncal structure in the male genitalia), alluding to the hooked subunci of this species.

**Comments on distribution and biology.** *Diaphanos curvignathos* occurs locally in Páramo de Ortiz, but is rare. It is possible that its distribution includes all of the páramos connected to the Niquitao massif, one of which is Ortiz. The latter range contains the highest mountains of Trujillo State, reaching 4006 m at Cerro La Teta.

Because of the orographic connection between the Mérida and Niquitao mountains and the fact that *D. huberi* ranges between 3400 and 4000 m in Mérida, it is possible that *D. curvignathos* and *D. huberi* are parapatric in the Niquitao range. However, *D. huberi* has been recorded only in the Cordillera de Mérida, and *D. curvignathos* is unknown from that range.

Owing to the reduced area of páramo above 3400 m in Niquitao, it is unlikely that any other species of *Diaphanos* occupies the uppermost level of these mountains, but further exploration is required.

All specimens but one, which was collected on my first visit to Páramo de Ortiz, were collected within a few minutes at midday, flying over

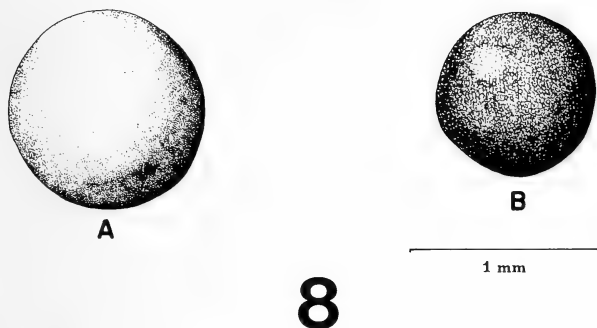


FIG. 8. Eggs of *Diaphanos* species. A, *D. fuscus*, B, *D. curvignathos*.

a small area of grasses in a bend in the road from Trujillo to Boconó. This visit was during the wet season and many plants, especially composites, were in flower. During a second visit in January (dry season), it was sunny but adult butterflies were rare. The butterflies were flying over the grasses and resting on the ground. The only female was taken resting on the dirt road at 1630 h, and it expelled one egg immediately upon capture. The egg (Fig. 8) was spherical (0.8 mm in diameter), pale green, vertically ribbed, and free of cement or glue. It is preserved and deposited in MBLUZ.

*Diaphanos curvignathos* has a relatively slow flight. It occurs only in páramo habitat between 2850 and 3100 m. The potential foodplant is an undetermined bamboo species (probably *Chusquea*) which is locally abundant in Páramo de Ortiz, especially near streams.

Other satyrids associated with *D. curvignathos* in Ortiz are *Altopedaliodes albonotata* (Godman) and an undescribed form of *Redonda empetrus*, all of which are sympatric.

#### DISCUSSION

There is sufficient evidence to conclude that *Diaphanos huberi*, *D. fuscus*, and *D. curvignathos* are three distinct species rather than subspecies. They differ in size, coloration, and genital structure. In general, *D. fuscus* is the largest and *D. huberi* the smallest. Differences in wing color patterns allow separation of the species following the key.

*Diaphanos fuscus* and *D. curvignathos* are most similar in external appearance, but genitalia suggest a closer relationship between *D. curvignathos* and *D. huberi*, both of which have well developed subunci. In contrast, the subuncus of *D. fuscus* is atrophied. *Diaphanos huberi* has a shorter saccus than the other two species. The valvae and aedeagus

are distinct in all three taxa, as are the shape of the wing scales (Fig. 6).

Apparently, each species is restricted to a small area of páramo, which may be the result of orographic and geographic isolation (Fig. 7). *Diaphanos fuscus* lives in the Cendé region whose páramos are quite isolated from the others in Venezuela. *Diaphanos curvignathos* lives in the highlands of Niquitao which are connected to those of the Cordillera de Mérida where *D. huberi* lives.

*Diaphanos huberi* has not been found in Niquitao, nor *D. curvignathos* in Mérida. Therefore, it appears that there are other ecological factors limiting their distributions. Although these two species inhabit only open lands of the páramos, *D. huberi* is restricted to the uppermost level between 3600 and 4000 m.

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CONTINUED INTERSPECIFIC HYBRIDIZATION BETWEEN  
*LIMENITIS (BASILARCHIA) ARTHEMIS ASTYANAX*  
AND *L. (B.) ARCHIPPUS* IN THE  
SOUTHEASTERN U.S. (NYMPHALIDAE)

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**ABSTRACT.** Interspecific hybridization between North American admiral butterflies is briefly reviewed and updated. Records of 77 wild male  $F_1$  hybrids between the viceroy, *Limenitis archippus* subspecies, and other nearctic *Limenitis* are noted. Among these are six new records of the hybrid form "rubidus" Strecker (*L. archippus*  $\times$  *L. arthemis astyanax*), including three each from two localities, one in Athens, Georgia and the other in northern Florida. Four of these new hybrids were reared from eggs and larvae wild-collected from willows (*Salix* spp.). Topics reviewed include 1) the present status of viceroy mimicry, and 2) the intense hybridization between phenotypically variable populations of *L. archippus* and *L. arthemis astyanax* observed recently in the Georgia/Florida region. Ecological, phenotypic, and behavioral reasons underlying this phenomenon are considered.

**Additional key words:** admirals, *L. archippus floridensis*, hybrid "rubidus," mimicry, selection.

Interspecific hybridization among North American *Limenitis* is well-known and has received much attention in the literature (see reviews by Platt et al. 1978, Platt 1983, Ritland 1990). Of particular interest to both lepidopterists and biologists are those crosses involving the viceroy, *L. archippus* (Cramer), a known mimic of various danaine models, and the other congeneric admirals with which *L. archippus* is broadly sympatric. These include butterflies of the eastern *L. arthemis-astyanax* complex (Platt & Brower 1968, Platt 1975, 1987a, 1994) and species of the two western complexes, *L. lorquini* Boisduval (Perkins & Perkins 1966, Gage 1970, Perkins & Gage 1970) and *L. weidemeyerii* Edwards (Cross 1936, 1937, Perkins & Perkins 1967, Simpson & Pettus 1976). Such crosses involving *L. archippus* and its congeners yield phenotypically intermediate  $F_1$  males, which are somewhat variable in terms of their relative light (orange) or dark (brownish-black) ground coloration, and also their partial postmedial white banding.

These naturally occurring hybrid forms have been variously named (see below), depending upon the species (or subspecies) involved. These interspecific hybrids are quite rare, usually occurring as from one to several specimens in widely distributed, but geographically isolated,



localities. Some of these locales are referred to by collectors as hybrid "hot spots." In such areas, low levels of interspecific cross-breeding take place over a number of years (and insect generations) in the same locality. Such wild hybrids presumably result from "stray" matings between individuals belonging to the two different taxa involved [e.g., 1) *L. arthemis arthemis*  $\times$  *L. archippus*, 2) *L. arthemis astyanax*  $\times$  *L. archippus*, 3) *L. weidemeyerii*  $\times$  *L. archippus*, and 4) *L. lorquini*  $\times$  *L. archippus*]. Including the specimens to be reported in this paper, a total of 77 published and unpublished records of such interspecific hybrids presently are known to the senior author. The most recent of these records are from south-central Louisiana in September 1991 (Kemp 1991) and southwestern Kentucky in September 1993 (Covell 1994, pers. comm.). These breakdown as follows:

- 1) hybr. "arthechippus" Scudder = 11 (including the type specimen of hybr. "rubrofasechippus" Gunder)
- 2) hybr. "rubidus" Strecker = 45
- 3) hybr. "weidechippus" Cross = 12
- 4) hybrid unnamed (*L. lorquini*  $\times$  *L. archippus*) = 9

All of these wild-caught specimens are males. However, a single heterosexual female specimen of hybr. "rubidus" has been lab-reared from Maryland strains (Platt & Harrison 1994). Similar female morphs occur in laboratory backcrosses involving the  $F_1$  hybrid males as well (Platt 1975, Platt et al. 1978).

#### Hybrid "rubidus" Strecker

Particularly well known are the  $F_1$  hybrids between the two mimetic butterflies, *L. arthemis astyanax* and *L. archippus* subspecies. Such hybrids are broadly distributed from Arizona and New Mexico across the mid-western U. S. into New England and south to Florida. The two parent insects belong to two separate well-known mimicry complexes, and themselves are very different in appearance (Figs. 1 & 4). Thus, the morphologically intermediate  $F_1$  hybrids represent a complete breakdown of both mimetic patterns (Fig. 3), and they quite likely are at a selective disadvantage from predation (by birds), when compared to either of the parental types. Because the known wild  $F_1$  hybrids all are males, they most certainly are at a mating disadvantage as well. The hybrid morphs are not known to persist in nature, and backcross specimens at present are known only from laboratory crosses (Platt 1975, 1983, Platt et al. 1978).

Presently, little is known regarding courtship behavior in nearctic admirals. Possibly visual, tactile, and pheromonal cues are important to the insects, as has been shown for closely related palearctic species

(Lederer 1960). Both parental species possess distinctive apical morphology of the male valvae (Platt et al. 1970), but apparently this pre-copulatory reproductive isolating mechanism is not perfect. The hybrids possess intermediate genitalic morphology.

Results of laboratory hybridization studies (Platt 1975, 1983) reveal that some degree of inter-fertility is possible in reciprocal crosses, although a greater number of the few interspecific pairings encountered in nature involve female *L. arthemis astyanax* and male *L. archippus archippus* (Klots 1959, Ritland 1990). Apparently, the specialized elongate, sickle-shaped valval tips of *L. archippus* subspecies are efficient mating structures which may play an important functional role in interspecific hybridization among the nearctic *Limenitis*. However, recent observations by Covell (1994) in southwestern Kentucky and by S. Mertens (pers. comm.) in north central Wisconsin, demonstrate that the reciprocal crosses involving female *L. archippus archippus*  $\times$  male *L. arthemis astyanax* and *L. arthemis arthemis* sometimes do take place in nature in the following article (Covell 1994:199).

### Present Status of Viceroy Mimicry

Recently, the queen/Florida viceroy relationship (and hence, by inference, the monarch/viceroy relationship as well) has been shown to be a Müllerian one, rather than a Batesian one, as classically believed (Brower 1992, Ritland 1991, Ritland & Brower 1991a, 1991b, Vane-Wright 1991, Walker 1991). These findings confirm those of J. V. Z. Brower (1958a, 1958b) and Platt et al. (1971) that certain avian predators (scrub jays, *Aphelocoma coerulescens coerulescens* Bosc. and blue jays, *Cyanocitta cristata bromia* Oberholser; Corvidae) find viceroy butterflies unpalatable in caged experimental situations.

### RESULTS

This paper reports the collecting of six additional wild "rubidus" hybrids, three each from Clarke Co., Georgia and Columbia Co., Florida. All were taken between 1973 and 1986 by J. R. M. The Athens records probably involve the nominate subspecies, *L. archippus archippus*, whereas those from Florida most likely involve the southern chocolate-brown subspecies, *L. archippus floridensis* Strecker, or *L. archippus/floridensis* intergrade forms, which are prevalent in northern Florida and southeastern Georgia. Four of these records represent specimens reared from wild-collected eggs and larvae found on willows (*Salix* spp.; Salicaceae). These records (presented chronologically) are as follows:

- 1) A worn adult male was collected at Belmont Road and Shoal

Creek in Athens (Clarke Co.), Georgia on 19 September 1973. The willow thicket was part of an ecotone habitat between the wooded bottomlands along Shoal Creek and an open cow pasture.

2) A fresh adult male was captured at the "Beaver Pond" site in Athens, on 17 May 1984. This area consists of a two- to three-acre beaver pond surrounded on three sides by open "old field" habitat, and by a mature pine plantation. The specimen was taken in a willow thicket between the beaver pond and the pine plantation.

3) A third hybrid male eclosed on 1 August 1984 from a single larva collected several weeks earlier on *Salix nigra* Marsh at the Athens "Beaver Pond" site.

4) Finally, three other male hybrids, all dark morphs of "rubicus," were among 12 admirals reared from a group of 11 young larvae and two eggs collected along a 30 m stand of willow shrubs (believed to be *Salix caroliniana* Michx.) between a service road and a cypress swamp, located just north of the entrance to O'leno State Park (Columbia Co.), Florida on 11 July 1986. At the time, the willow leaves showed few signs of larval feeding, and only one freshly eclosed light orange female *L. archippus archippus* was seen flying in the area.

This collection of eggs and larvae was made between summer broods of the adult admirals. Only 12 butterflies were reared, since one of the eggs failed to hatch. These insects were lab-reared at room temperature on *Salix nigra*, and eclosed between 19 July and 5 August 1986. Ecllosion dates for the three hybrids were 19, 23, & 29 July. Also, reared in this sample were seven *L. arthemis astyanax* (4 males & 3 females) and two male *L. archippus floridensis*. All except one male *L. arthemis astyanax* represent the iridescent greenish form "viridis" Strecker.

#### Intense Hybridization in the Florida/Georgia Subspecific "Suture-zone"

Assuming that all like butterflies were siblings, the 12 individuals must represent eggs laid by at least three different wild females. The last three hybrids well may involve the dark brown Florida subspecies of *L. archippus* (Fig. 2), although specimens seen and taken at this locality represent intraspecific intergrades, and vary greatly in ground color (ranging from bright orange to orange-brown to brown). This region, of course, represents an area of intergradation between the typical orange colored eastern viceroy and the darker peninsular subspecies *L. archippus floridensis* (Remington 1958, 1968).

Ritland (1990) reports seven additional hybr. "rubicus" records from Georgia and northern Florida obtained in 1986 and 1987. Five of his records, likewise, were obtained from wild-collected larvae taken on *Salix caroliniana*. There are, in addition, two earlier records of hybr.

"rubicus" from this region (Platt et al. 1978). All 13 of the wild "rubicus" hybrids recently collected by J. R. M. & D. B. R. from this area represent progeny of either spring or early summer interspecific matings of the parental butterflies. Further north, and in western regions of the country, the majority of such crosses seem to occur in the late summer or fall (Platt 1987b). According to Ritland (1990), *L. arthemis astyanax* is absent from local habitats where *L. archippus archippus* and *L. archippus floridensis* fly during the late summer and fall seasons.

Ritland (1990) discussed possible reasons for this cross-breeding. They include the following:

1) The existence of the subspecific intergrade zone between *L. archippus archippus* and *L. archippus floridensis* in southern Georgia and northern Florida, which creates greater genetic and phenotypic variability within populations of this often phenotypically uniform species. This greater genetic diversity within these viceroy populations may contribute to more labile female mate-choice.

2) The general scarcity of *L. arthemis astyanax* in many regions of Florida, at least relative to *L. archippus archippus*, and the utilization of similar microhabitats by both species in the southeastern U.S., especially during the early part of the year (April-June). [However, in northern Florida, *L. arthemis astyanax* populations can be reasonably common, locally.]

3) In this area *L. arthemis astyanax* switches to greater dependence on salicaceous foodplants, since its main rosaceous foodplants, such as *Prunus serotina* Ehrh., become restricted to dry woodland habitats, and generally do not occur in the moist open meadow habitats, usually frequented only by viceroys.

## DISCUSSION

Our present studies reveal the existence of phenotypic intergradation between *L. archippus archippus* and *L. archippus floridensis* in Georgia and northern Florida, as reported previously by Remington (1958, 1968). In fact, viceroy populations as far north as Athens, Georgia show tendencies toward this phenotypic blending with the darker southern subspecies. Such individuals usually are a darker orange-brown color than that of nominate *L. archippus*. Many of these specimens have forewings that are a shade darker than their hindwings, and some even possess ventral hindwing basal orange spots, like those characteristic of *L. arthemis astyanax* (Fig. 1). This last trait appears in *L. archippus archippus* because of differences in hues of the ventral hindwing ground color and of the basal spots themselves. Laboratory crosses between the two viceroy subspecies clearly show that the appearance of these ventral

## DORSAL



## VENTRAL

FIGS. 1-4. Specimens of the different forms of *Limenitis* from the southeastern U. S. 1) *L. archippus archippus*, no. 84-1, Athens (Clarke Co.) Georgia, Aug. 1984, J. R. M.; 2) *L. archippus floridensis*, no. 86-7, eclosed 3 Aug. 1986; 3) hybr. "rubidus", no. 86-11, eclosed 23 July 1986; & 4) *L. arthemis astyanax*, no. 86-3, eclosed 27 July 1986. All four specimens are males, reared on *Salix* sp. Specimens 2-4 reared from eggs and larvae collected on *Salix* sp. near O'leno State Park (Columbia Co.), Florida, 11 July 1986, by J. R. M. All specimens deposited in the insect collection at U.M.B.C.

basal spots can occur without any cross-breeding involving viceroys and red-spotted purples. Thus, in itself, this trait among viceroys is not an indicator of such interspecific genetic introgression.

Although throughout much of Florida *L. arthemis astyanax* seems to be relatively scarce compared to *L. archippus*, this does not appear to be the case in the O'leno State Park region of northern Florida. This area includes mesic habitat laced with ribbons of wet bottomlands and sink holes. These wetter low areas usually are wooded. The higher, more dry uplands form a patchwork of open fields, farmlands, and islands of either pines (*Pinus* spp.; Pinaceae) or oaks (*Quercus* spp.; Fagaceae). Within the more open pine areas and throughout the old fields, wild cherries and wild plums (*Prunus* spp.; Rosaceae) are among

the most common successional tree species. Willows (*Salix* spp.) are much less common and are restricted to the wettest locales. Thus, *L. arthemis astyanax* usually is common and widespread around O'leno State Park, whereas *L. archippus* (both subspecies and their intergrades) is only locally abundant. Consequently, the interweaving of the two habitats quite likely plays the most important role in bringing the two species together in this area. The greater utilization of salicaceous foodplants by *L. arthemis astyanax* larvae has not been demonstrated, and, in fact, seems less likely to us as an important mechanism for bringing the two species together. It is true, however, that virtually all hybr. "rubidus" have been collected in rather open moist field or ecotonal areas, having willows and water nearby. Such localities generally are considered to be viceroys habitats.

An additional contributing factor to finding so many hybrids in such a short time period may be the increased intensity of collecting wild admiral larvae. This by itself has yielded nine (69%) of the 13 hybrids recently taken. Nearly all previous specimens were collected with hand-nets, following "random" encounters with collectors. At the same time, such rare insects are eagerly sought, and are collected whenever possible. In other words, the frequency of these cross-matings may not be just a recent phenomenon, but may have been occurring all along over a prolonged period of time. Such crosses simply may be an indication of the extremely close affinities between *L. arthemis astyanax* and *L. archippus* subspecies, as belied by their very similar developmental stages. It is likely that the red-spotted purple (*L. arthemis astyanax*) has evolved as a mimetic form from *L. arthemis arthemis* in comparatively recent times. Thus, it may have spread southward into the vicinity of northern Florida very recently (geologically speaking) as well.

Four of the hybr. "rubidus" specimens collected by J. R. M. are in his personal collection. The other two hybr. "rubidus" and the remaining Florida specimens are in the U.M.B.C. insect collection.

#### CONCLUSIONS

Evidently, both the Beaver Pond site in Athens, Georgia, and the O'leno State Park locality in northern Florida represent the interspecific "hot spot" locales referred to earlier in this paper. In such habitats, ecological conditions including temperature, light, moisture, and food plant types and distributions, together with the relative abundances of the two parental species (with one being prevalent, but the other much scarcer) produce conditions leading to "microsympatry" at certain times of the year (Ritland pers. comm.). As long as such conditions persist,

elevated levels of hybridization can continue to occur at these specific locales.

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FIELD OBSERVATIONS OF MATINGS BETWEEN FEMALE  
*LIMENITIS ARCHIPPUS* AND MALE *L. ARTHEMIS*  
SUBSPECIES (NYMPHALIDAE)

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**Abstract.** Natural matings of female viceroy butterflies, *Limenitis archippus*, with males of *L. arthemis astyanax* in Kentucky and *L. arthemis arthemis* in Wisconsin are described and illustrated. These are the first field reports of female *L. archippus* paired with male *L. arthemis*. The interspecific pairing observed in Kentucky, plus the collection of two hybrid male “rubidus” Strecker at the same site in September 1980 and 1993 suggest a high level of hybridization at that site. This seemingly high frequency is discussed in light of recently advanced hypotheses.

**Additional key words:** *Limenitis arthemis arthemis*, *L. arthemis astyanax*, hybridization.

Natural hybridization among North American butterflies is apparently uncommon, except between *Colias eurytheme* and *C. philodice* (Silberglied 1973). However, hybridization recently has been observed with some frequency in the highly mimetic admiral butterflies *Limenitis archippus* (Cramer) and *L. arthemis* (Drury). The viceroy (*L. archippus*) has evolved appearance and behavior modeled after the monarch, *Danaus plexippus* (L.), and in Florida, the queen, *D. gilippus* (Cramer) (Ritland 1990). *Limenitis arthemis astyanax* is a Batesian mimic of the pipevine swallowtail, *Battus philenor* (L.) (Papilionidae), within the range of that swallowtail, grading northward to the non-mimetic, white-banded subspecies *L. arthemis arthemis*. Mimicry in these two eastern *Limenitis* species has been studied extensively in the laboratory (Platt & Brower 1968, Platt 1983). Platt et al. (1978) reported records of 10 wild-caught hybrids resulting from *L. archippus* × *L. arthemis arthemis*, known as “arthechippus” Scudder, and 24 “rubidus” Strecker—the F<sub>1</sub> hybrid of crosses between *L. archippus* and *L. arthemis astyanax*. Platt (1987) raised the number of both hybrids to 32, and Platt and Maudsley (1994) increase the number to 45. All known wild-caught hybrids are males.

Collections and Observations in Kentucky and Wisconsin

One of the records listed by Platt et al. (1978) was from Jefferson County, Kentucky, collected by R. Steilberg and J. Smith in September 1948. That specimen is apparently lost. Three additional specimens have been taken more recently in Kentucky, and are in the University of Louisville collection. The late Siegfried Scholz collected one of these at Waverly Park near Valley Station, Jefferson County, on 21 October 1978. I took another on the banks of the Mississippi River at Hickman,



Fulton County, Kentucky, on 14 September 1980. On 7 October 1989, at 1725 h, I encountered a nearly fresh female *L. archippus* mating with a ragged male *L. arthemis astyanax* (Fig. 1). This occurrence was only about 300 m south of the 1980 capture location. Robert V. Gregg also took a hybrid at the exact same site on 11 September 1993 (Figs. 3, 4).

Temperatures on the September capture dates in 1980 and 1993 were moderately high, and many pierids and other butterflies were recorded on those days. The day of the mating event in 1989 was cool, reaching a high of only about 17 degrees Celsius. Several other female viceroys were on bushes and trees nearby in basking postures. While not quantified, there were significantly more *L. archippus* than *L. arthemis astyanax* at the site. Abundant willow (*Salix* sp.; Salicaceae) was growing along the Mississippi River bank there, but I did not notice any *Prunus* species (Rosaceae). Very few butterflies of other species were still active.

The mating pair was photographed by W. R. Black, Jr., and we observed the phenomenon until 1740 h when I decided to capture the paired insects. As soon as I approached them with a net, the female flew upward, carrying her mate with her. After attaining a height of about 45 m, she descended into a small tree, barely within reach of my net. After capturing them I placed the pair in a Ziploc bag where they continued mating until dark, an hour later. I took them back to Louisville, but found them moribund next morning. The female could not oviposit because a dried fluid (presumably hemolymph) had covering the posterior part of her abdomen. I dissected out several of the eggs but none hatched.

In personal correspondence about this occurrence with A. P. Platt, I learned that this was the first field observation of a female *L. archippus* mating with a male *L. arthemis astyanax*. Later Platt informed me of a female viceroy seen mating with a male *L. arthemis arthemis* in Rusk County, Wisconsin (Fig. 2). In this case, photographs were taken by Steven Mertins of Ixonia, Wisconsin, after the discovery of the pair by his son Jake. The Mertins informed Platt that the mating was observed in "mid-afternoon" at the "end of August 1988." They did not collect the butterflies. This occurrence is the earliest record of a female *L. archippus* involved in interspecific mating. Platt et al. (1978) report

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FIGS. 1-4. 1, Female *L. archippus* mating with male *L. arthemis astyanax*, Hickman, Fulton County, Kentucky, 7 October 1989; 2, Female *L. archippus* mating with male *L. arthemis arthemis*, Rusk County, Wisconsin, August 1988; 3, Upperside of *L. archippus* × *L. arthemis astyanax* ("rubidus"), Hickman, Fulton County, Kentucky, 11 September 1993; 4, Underside of specimen shown in 3.

three captures in Wisconsin of hybrid male "rubidus" with features similar to Kentucky specimens (Figs. 3, 4).

## DISCUSSION

The apparent frequency of hybridization in *Limenitis* at the western Kentucky site may lend support to hypotheses proposed by Ritland (1990). He pointed out that while records of hybrid admirals are rare over most of their sympatric ranges, there were 7 "rubidus" recorded (2 seen or captured, and 5 reared from captured larvae) from a zone in southern Georgia to northern Florida during a 13-month period. Ritland also observed matings in nature between female *L. arthemis astyanax* and male *L. archippus* there. He indicates that these observations "provide evidence of mate-choice breakdown"—i.e., careless mate selection by *L. arthemis astyanax* females and consequent hybridization. This phenomenon may be more common in the southern Georgia/northern Florida area than elsewhere in their mutual ranges, as supported by additional evidence presented by Platt and Maudsley (1994). Ritland gives possible explanations as (1) more frequent matings between these species there than elsewhere, and (2) mating frequency not greater there, but  $F_1$  hybrids "more viable than those elsewhere." Segregation of the species by habitat determined by different foodplants is mentioned as a means of pre-mating segregation. Ritland points out that in his study area, there is little wild cherry—the usual foodplant of the red-spotted purple—and that the larvae feed on willows alongside *L. archippus*. Platt and D. Flaim have observed the larvae of *L. arthemis* subspecies feeding on Salicaceae in Maryland and New England as well. Midsummer senescence of wild cherry leaves could lead to increased oviposition on willows by *L. arthemis astyanax* by midsummer females producing the southern fall brood. This explanation would not hold for the hybrids reported by Ritland (1990) and Platt and Maudsely (1994) that eclosed prior to August.

A third possible explanation is that the Georgia/Florida area represents an intergrade zone between the northern orange *L. archippus archippus* and the dark brownish Florida viceroy, *L. archippus floridensis* (Strecker) that mimics the queen, *Danaus gilippus* Cramer, instead of the monarch. In that area, normal mate selection behavior could be less discriminating, and *L. arthemis astyanax* may mate more readily with *L. archippus*.

Against this background, the observation of one interspecific mating and two specimens of "rubidus" within the space of about five riverine acres in western Kentucky seems to lend support to the following conditions mentioned by Ritland as characteristic of a "hybridization hot spot."

(1) Abundant willow but no black cherry were observed at the site (although black cherry could exist in some nearby woodland, subject to flooding as occurred in the summer of 1993).

(2) Many more *L. archippus* than *L. arthemis astyanax* were seen at the site on each visit in September or October. The viceroy outnumbered the red-spotted purple on 11 September 1993 by a ratio of 10:1 (W. R. Black, Jr. pers. comm.).

The first observation seems to qualify as what Ritland (pers. comm.) calls the "unusual habitat explanation." With respect to probable use of willow as a larval foodplant by both species, the Fulton County, Kentucky site seems to match parts of the Georgia/Florida hybridization zone. Perhaps *L. arthemis astyanax* that mate successfully with *L. archippus* in the Kentucky site fed as larvae on willow rather than wild cherry. If so, pheromones of the two species might be more similar and isolating mechanisms diminished than if *L. arthemis astyanax* fed on wild cherry. In September and October very few *L. arthemis astyanax* were seen at that site, while the viceroy was common. Male *L. arthemis astyanax* might court female *L. archippus* in the absence of sufficient females of their own species.

Less applicable to the Kentucky case is Ritland's hypothesis that a higher rate of interspecific interaction might occur where viceroy wing color is unstable, as in the Georgia/Florida sites described by Ritland and by Platt and Maudsley (1994). Platt indicates viceroys with the contrastingly dark forewings can be found as far north as the Great Dismal Swamp on Virginia's coastal plain. I have found very few individuals with forewings darker than hindwings in Fulton County, Kentucky, and none with red spots on the underside as mentioned by Platt and Maudsley (1994).

I cannot affirm that the frequency of hybridization between the two admiral species in Fulton County, Kentucky, approaches that reported from the Georgia/Florida habitat. However, three observations of such activity during a total of less than 12 hours of observation (1980–1993) over several seasons seems to indicate rather high frequency there.

Platt et al. (1978) mention the prevalence of hybrid admirals occurring in late summer to early fall—toward the end of the flight season northward. The Kentucky observations and collections support that observation.

My observations in Kentucky lead me to agree with Ritland (1990: 171): "These arguments remain speculative because mate choice in viceroys and red-spotted purples is poorly understood; however, the proposed mechanisms identify several avenues of research that should be pursued in attempting to explain the elevated hybridization in this area." The definition of hybridization "hot spot" should emerge as more field data are collected and assimilated.

## ACKNOWLEDGMENTS

I thank A. P. Platt for providing the Wisconsin data and photos, and for his helpful comments. Thanks are due also to Jake and Steve Mertins for providing their color photograph from Wisconsin; to R. V. Gregg for donating his "rubidus" specimen to the University of Louisville Insect Collection; and to W. R. Black, Jr., and Scouts of Troop 1, Paducah, Kentucky, for their assistance. My thanks also to L. P. Brower and D. Ritland for comments on the manuscript.

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## A TECHNIQUE FOR SETTING AND MOUNTING MICROLEPIDOPTERA

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**ABSTRACT.** Freshly collected and ammonia-killed microlepidoptera, pinned on minutenens, are spread in small, shallow, plastazote-lined boxes with grooves, using either small card points mounted on short pins or translucent setting paper strips to hold the wings. The method produces high-quality specimens, is fast, and uses compact, light-weight, inexpensive equipment. The method is also versatile in that any desired quality of setting, from preliminary, partial setting to the finest setting, can be attained with the same equipment with equal efficiency under any condition, whether at home or on collecting expeditions. The main steps of the method are illustrated. A technique for staging minutenens-pinned specimens is also presented.

**Additional key words:** spreading box, staging, double-mount, ammonia.

During the past 90 years, several papers have presented, with various amounts of detail, techniques for preparing (pinning, setting, and mounting) microlepidoptera (e.g., Kearfott 1904, Calmbach 1921, Lhomme 1926, 1927a, 1927b, Amsel 1935, Holland 1937, Janse 1939, Janmouille 1943, Charlson 1945, Lindquist 1956, Hodges 1958, Lewis 1965, Tagestad 1974, Zimmerman 1978, Sokoloff 1980, Mikkola 1986). However, our contacts with many lepidopterists indicate that, at least in North America, good and simple techniques for preparing microlepidoptera are not well known. In fact, many North American lepidopterists do not even collect microlepidoptera as routinely as other Lepidoptera, in part because of the perceived inconvenience of preparing them. Microlepidoptera that are collected are often only the larger specimens, in groups such as pyraloids, tortricoids, and large gelechioids.

The paucity of good quality microlepidoptera from North America in many collections is one of the causes for the very slow progress in systematic studies of the Nearctic fauna. Our knowledge of the taxonomy and faunistics of many families of microlepidoptera is shockingly poor. A plea recently has been made for North American lepidopterists to take on the collection and study of microlepidoptera (De Benedictis 1993). Of course the first step in this endeavour is to acquire a *good and efficient* technique for preparing specimens.

There are probably nearly as many ways of preparing microlepidoptera as there are individuals collecting them. The basic method of spreading microlepidoptera is the same as for larger Lepidoptera. How-

ever, some adjustments, both at the time of collecting and of preparation, and in the equipment, are needed because of the small size and fragility of microlepidoptera.

Over the years we have tried every different method and variation of preparation for microlepidoptera that we came to know. While most techniques can yield high-quality specimens, many suffer from being relatively slow or requiring somewhat cumbersome equipment (e.g., spreading boards) ill-suited for prolonged field work under difficult conditions. We sought to develop a technique that offsets these problems, i.e. one that is rapid and usable under any condition with equal efficiency, yet versatile with respect to the quality of preparation desired by the collector. An earlier version of the technique described here was published in French by Landry (1991) but we have modified it slightly, with some additions.

Our method actually combines elements from other methods employed by microlepidopterists, with added refinements. It is based on the concept of setting microlepidoptera on the bottom of a box, which can be traced back at least to Amsel (1935). Modern materials, especially dense polyethylene foam, dramatically enhance the results of Amsel's method. Partial spreading in such boxes is now used by many microlepidopterists on collecting trips (Zimmerman 1978:50–59, Nielsen 1980). The main shortcoming of partial spreading is that special specimens, such as types of new species or those needed for photography, may need subsequent relaxation for final spreading. The technique exposed here offers the possibility of a full range of quality of preparations, from unspread to fully spread with as much care as a perfectionist may wish, all with the same equipment and with hardly any extra time. The technique may be used in the field, in the lab, or at home. The necessary equipment is very compact, light-weight, inexpensive, and easily made. We have tested the method with tens of thousands of microlepidoptera over the past few years, under conditions varying from local day trips to month-long expeditions in the tropics (including camping).

In addition to the actual technique of setting microlepidoptera, we offer some suggestions for handling specimens when they are collected in the field, and for staging (double-mounting) spread specimens. Appropriate handling of collected microlepidoptera is as critical as the actual setting in obtaining high quality specimens, and so is the final staging to insure safe preservation in subsequent handling.

#### COLLECTING

The facility and rapidity of the technique outlined here rests on working with the freshest specimens possible. Moths are placed indi-



vidually in glass vials upon collecting and kept *alive* until the time of pinning and setting. Upon returning from the field, vials are stored in a cool, dark place if the specimens cannot be prepared immediately. The ideal place is the refrigerator, or a cooler box if one is on a prolonged field trip. We have been able to keep specimens alive for up to five days in this manner, although we recommend delaying as little as possible (some moths will begin to show some wear even after 1–2 days in the refrigerator). Refrigeration is particularly useful if one has had a large catch on one day and there is not enough time to prepare all specimens immediately after they have been collected. We recommend preparing the smallest microlepidoptera as soon as possible, as they will die more quickly from dehydration. Once dead, small moths tend to dry very quickly and become difficult to relax and spread. In the humid tropics, small microlepidoptera will dehydrate quickly inside vials (often in just a few hours) and are best set as soon as possible. Always begin by preparing the smallest specimens first, working up to larger ones. Refrigeration, even if available, should probably not be used for tropical microlepidoptera from those regions that seldom experience temperatures below 10°C, because the relative cold will kill many of them.

**Vials.** Collecting vials should preferably be made of glass and close with an easily removable stopper that can be opened with a single hand (the other may be busy holding a net). We use glass vials that are 65 mm long and 19 mm in diameter, closed with a rubber stopper. Stoppers should be as little wedge-shaped as possible, otherwise smaller microlepidoptera will crawl in the space between the stopper and the vial neck and damage themselves. We carry about 100 vials for most day-time collecting, at least twice as many for night-time collecting at a light. Experience will dictate the adequate supply. During day-time collecting, care must be taken that the vials are not exposed directly to or heated by sunlight, otherwise the moths will quickly die and dry. If possible, avoid plastic vials (snap-cap type), especially with the smaller specimens, because the static charge that such vials accumulate through handling and friction will damage the squamous cover of the moths and increase the rate of wear.

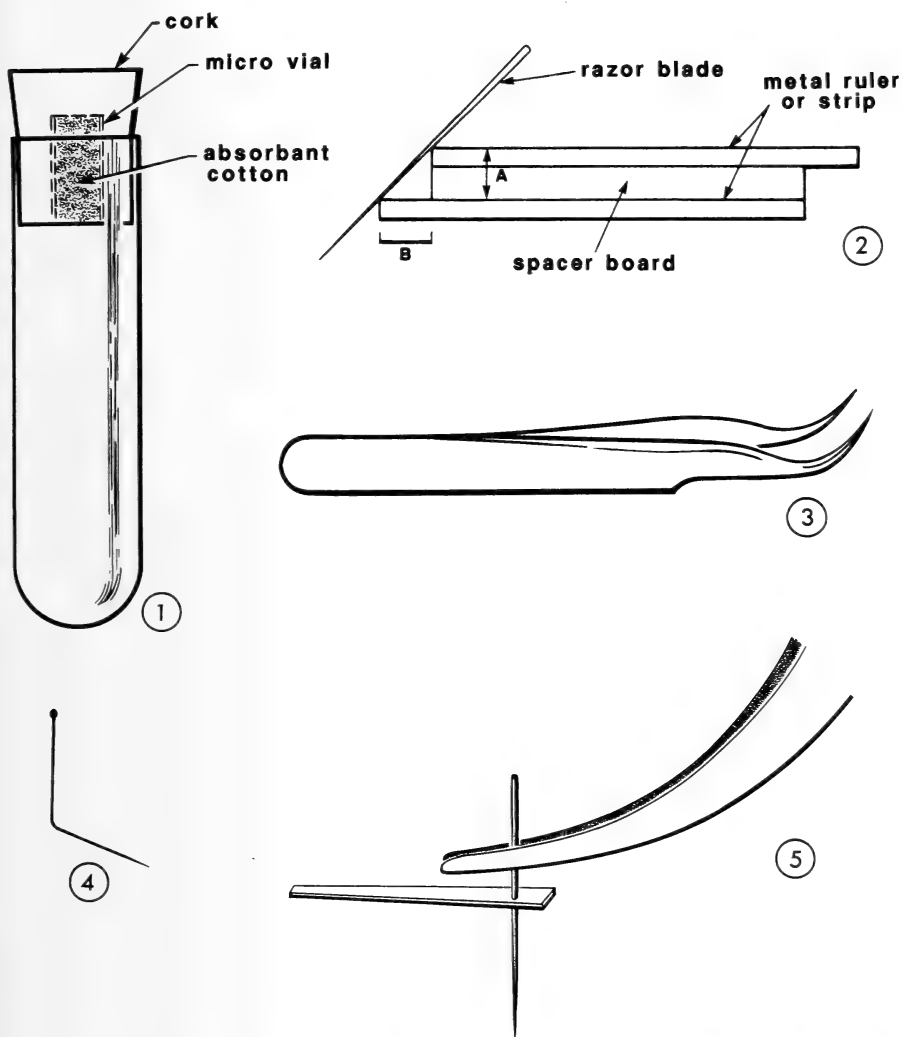
A word of caution is necessary if one is setting reared specimens: *never* set a freshly emerged moth. Allow at least 24 hours (longer if a genitalia dissection may be required) for the moth to harden sufficiently. Without this precaution, wings may curl, crumple, or droop after removal from the setting box, and if the genitalia are later dissected, structures will be insufficiently sclerotized and difficult to prepare adequately.

## POISON AND KILLING TUBES

The choice of poison is, of course, a matter of personal preference, availability, etc. We strongly recommend ammonia (ammonium hydroxide): it has a quick knock-down action and leaves freshly killed specimens beautifully relaxed and ready to be spread immediately with the greatest ease. We have tried other killing agents and methods, but ammonia is the one that has given us the best results. The ammonium hydroxide solution should be as concentrated as possible. A laboratory-grade solution containing about 30% ammonia and 70% water is preferable because it has a very fast knock-down action. Household ammonia, generally a murky liquid, is weaker and unsuitable.

For killing tubes, we use glass tubes closed with cork stoppers into which a small microvial is inserted, loosely stuffed with cotton (Fig. 1). Five to ten minutes before using a tube, the cotton is imbibed with a few drops of ammonia solution, and the tube closed to let the ammonia concentration rise. This type of killing tube offers nothing inside against which struggling moths may rub; the disadvantage is that the tubes need to be recharged more frequently, approximately once every 2–3 hours of continuous use (when opened several times periodically). When setting large numbers of microlepidoptera, we use up to 10 tubes at a time to minimize recharging, and place only 2–3 moths per tube at a time. It is essential to check for and wipe traces of moisture or sweating on the walls of the killing tubes. Charged tubes may be laid on their side to prevent any ammonia from possibly running down the sides, although this will not be a problem if a modest quantity is used. When tubes are not in use for more than a day or so, it is preferable to leave them open and remove the cotton swab from the stopper to allow them to dry thoroughly.

Ammonia has a few disadvantages: it tends to sweat in a tube if an excessive quantity is used or if it is too warm (tubes must not be exposed to heat or direct sunlight)—but this is a disadvantage common to most liquid poisons; it loses strength relatively rapidly in a frequently open tube; and fumes are choking, irritating. Weak ammonia must *not* be used for moths with green, red, or orange pigments because the long exposure needed to kill them may cause discoloration. If the ammonia is strong though, this is not a problem providing that the moths are removed as soon as they are dead. In case of doubt about possible discoloration, one should use another poison, preferably ethyl acetate (subsequent relaxation may be necessary). With strong, concentrated ammonia, we have not had discoloration problems. Generally we have found that the advantages of ammonia far outweighed its disadvantages, none of which presented a real problem if it was used with the pre-



FIGS. 1-5. Materials required for preparing microlepidoptera. 1, Killing tube; 2, superimposed, offset rulers to cut symmetrical V-shaped grooves,  $A = B$  for  $45^\circ$  grooves; 3, curved forceps used to handle minutens; 4, bent standard pin used to assist pinning and spreading; 5, card triangle mounted on shortened pin used to hold set wing in the point method.

cautions outlined above, and that it was no more inconvenient to use than any other poison.

Recently we have experimented with a solid form of ammonia, ammonium carbonate, a salt with the appearance of cyanide crystals. Upon

contact with the ambient humidity, the crystals decompose into gaseous ammonia, carbon dioxide and water vapor (Gilligan and Gilligan 1990). Killing tubes are made simply by packing a 1–2 cm thick layer of crystals in the bottom and covering them with a smooth, porous material [e.g. artificial foam sponge (Gilligan and Gilligan 1990)]. We used plastic caps (from snap-cap vials) punctured with many minute pin holes to cover the crystals. Plaster cannot be used because the water it contains will instantly dissolve all the crystals and produce all the ammonia at once. We obtained satisfactory results with ammonium carbonate if used for small numbers of specimens. Disadvantages are that the rapidity of killing decreases markedly compared to liquid ammonia if one opens the tubes frequently; also if there are too many specimens in a tube and it is warm, the moisture content may rise to the point where, upon cooling, crystals may form on the specimens; such crystals are then very difficult to remove. For these reasons we find ammonium carbonate less satisfactory than ammonium hydroxide.

Ethyl acetate also works well but we found that it has a tendency to stiffen many microlepidoptera if they are left in the killing tube a few minutes too long; hence, some relaxation is sometimes necessary. Like ammonia, it is volatile, and tubes need frequent recharging and may “sweat” if heated. It is also flammable and will dissolve some plastics. Generally, we have found ethyl acetate to be less satisfactory than ammonia in quickly producing ready-to-spread specimens.

### KILLING

Remove the cork, insert one moth, close the cork. Repeat with other tubes. When there is one moth in each tube, start again with the first tube, ensuring that the moth is stunned. Continue until there are 2–3 moths per tube. Stunning takes less than five seconds when the ammonia is strong but may stretch to 10–15 seconds after tubes have been opened several times. Moths should be left in the killing tubes for at least 15 minutes to ensure they are dead. Very small moths (Nepticulidae, small Gracillariidae, for example) can be removed sooner. A time saving strategy in the subsequent setting operations is to segregate specimens by size at the killing stage. This way, at the setting stage, one does not have to switch back and forth among various spreading boxes with different groove widths.

### SETTING EQUIPMENT

**Spreading boxes** (Figs. 6, 17–18). We use shallow, clear polystyrene plastic boxes; currently we have two sizes, 11cm × 11cm × 2cm, and

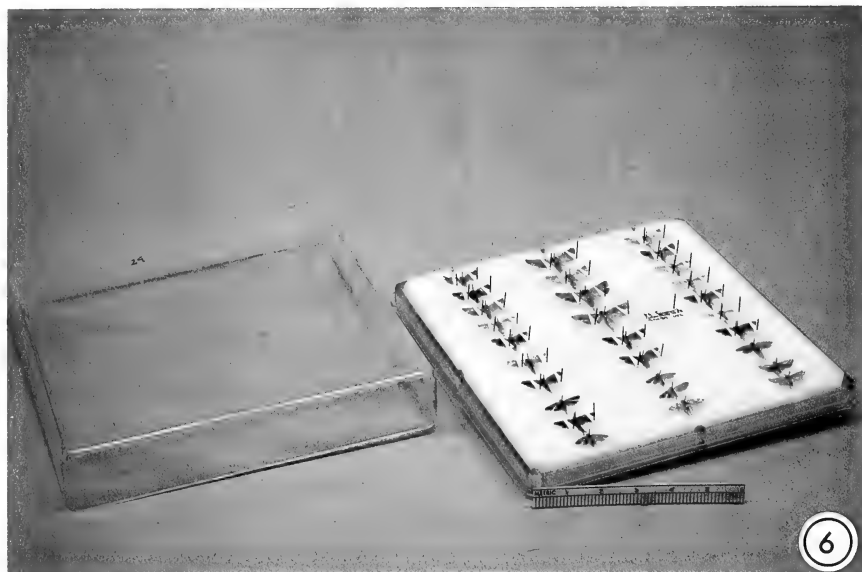


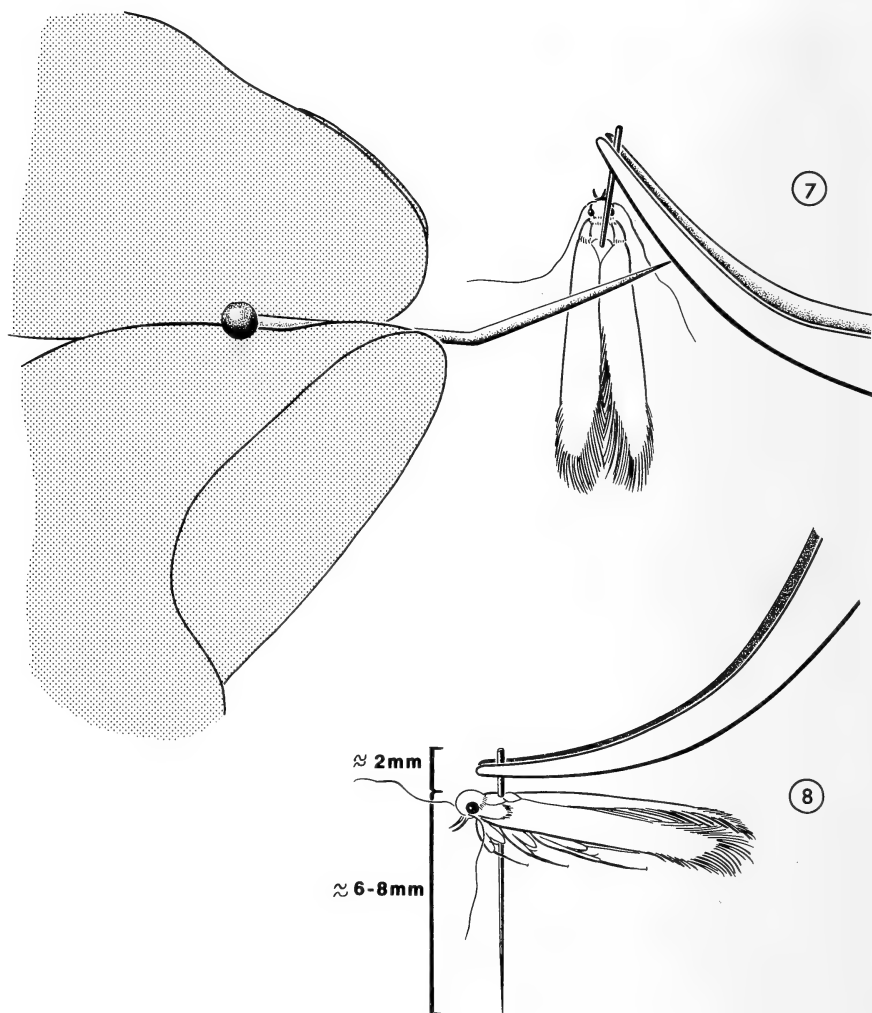
FIG. 6. Spreading box. The actual lid is used as bottom on which the plastazote is glued. Scale in cm.

12cm  $\times$  8cm  $\times$  2cm, obtained from different suppliers. Actual dimensions are not important, as long as boxes are relatively small, preferably shallow (for compactness), with a low-edge lid, rigid, and relatively airtight (or pest-proof).

For a spreading surface we use Plastazote®, a dense, smooth polyethylene foam. We found this material best because it affords the following advantages: the surface acquires a small static charge through handling, which helps wings cling slightly and facilitates spreading; it grips the pins firmly and leaves no pin holes; it sustains hardly any wear.

A 1-cm thick piece of plastazote is glued inside the lid of a spreading box (we use all-purpose, non-toxic white glue). Gluing the foam inside the lid (using the bottom as lid) eliminates edges to the spreading surface, greatly facilitates work of the hands, and maximizes use of the spreading surface.

Before gluing the foam into the boxes, we cut three or four V-shaped grooves with a razor blade. To obtain grooves with perfectly symmetrical sides, we use two metal rulers or strips, with one being taped on top of the other and propped up by a thin board; the edge of the top ruler is offset from the edge of the lower one by a distance equal to that of the ruler + board thickness (Fig. 2). To cut, the blade is slanted



FIGS. 7-8. 7, Inserting the minuten while holding the body with a bent standard pin; 8, Minuten-pinned specimen, showing approximate height on 1-cm long minuten.

and abutts both edges. Symmetrical grooves facilitate spreading. We use a series of spreading boxes with various groove widths, these varying from 1-5 mm (2mm and 3mm are the most frequently used widths). It is not necessary to have square grooves with vertical sides, as on standard spreading boards. In fact, the sides of V-shaped grooves often provide direct support for the abdomen.

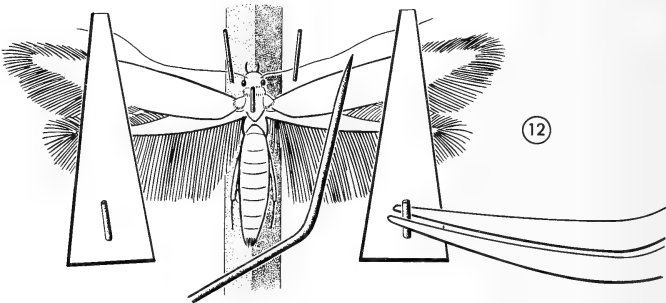
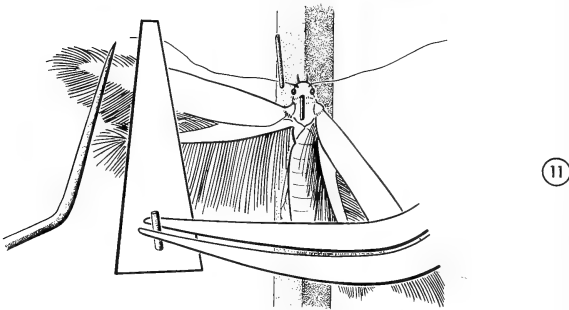
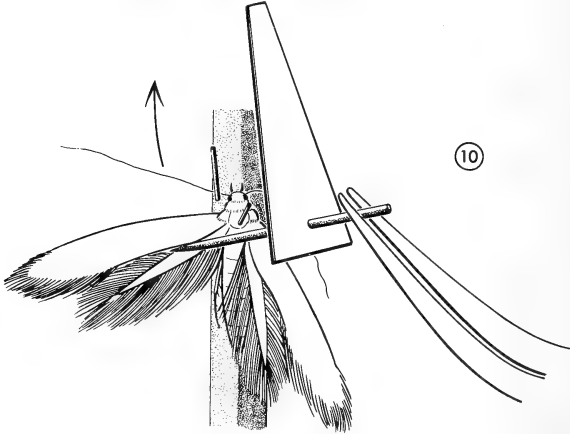
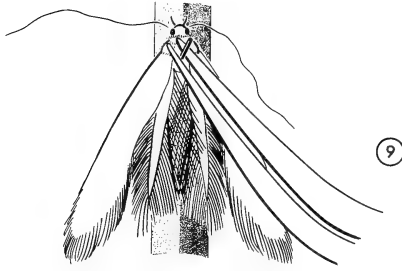
**Minuten pins.** Use of minuten pins involves subsequent staging or

double-mounting, so this is distasteful to many a lepidopterist. Whatever the perceived difficulty, inconvenience, or time factor involved, we emphasize that this is by far the best and safest way of obtaining fine-quality microlepidoptera. Double-mounted specimens can sustain rougher handling without damage and are far less likely to lose their abdomen, a very frequent problem with microlepidoptera that are mounted on fine standard pins (00 or 000), which are very springy. The genitalia are critical for the specific determination of numerous species of microlepidoptera, hence the abdomen must not be lost.

There are different qualities of minutens available on the market. For the best results, and to avoid frustration, one should use the best quality stainless steel minutens. Avoid black-enameled minutens, which have a tendency to rust (guaranteed if one is in the tropics) and have tips that more easily "hook" (being made of softer metal). The difference in price between stainless steel and black-enameled minutens is small. Diameters of the most useful sizes are 0.20 mm, 0.15 mm, and more rarely 0.10 mm (for nepticulids and other tiny microlepidoptera); some British brands label their minutens A1 (0.14 mm) and B1 (0.19 mm) (1 referring to the shortest length, usually 10–12 mm).

Most minutens are excessively long and must be shortened down to no more than about 1 cm for the larger ones (0.20 mm) or 6–7 mm for the finer ones (0.15 mm and 0.10 mm). If minutens are not shortened, the excess length jutting either above or below the specimens will greatly increase the risk of breakage or damage during handling of the double-mounts (fingers pinching the minuten while grasping the stage-supporting pin will spring the specimen and likely send parts flying, most commonly the weakly-attached, all-precious abdomen). A rapid method of shortening a large number of minutens is to cut narrow strips of plastazote (often the latter's thickness is conveniently 1 cm or 7 mm), to insert minutens all the way through the strips (ensuring that their tips do not extrude), and trimming off the excess length close to the strip surface with good scissors or pin cutters. To maximize efficiency later in the setting process, we prepare large quantities of trimmed minutens in advance. Minuten-loaded plastazote strips can be packed side by side in an insect mounting tray or small shallow cardboard box. A protective layer of plastazote is glued on the bottom of the tray or box. Strips are then laid upright, side by side, and held in place with pins inserted through the sides of the tray or box; any remaining space can be filled with plastazote. Use a box narrow enough for the holding pins to pierce through at least half of the strips from one side.

**Tools.** We use curved forceps for handling minuten pins (Fig. 3). The inner surface of the grasping end must be smooth (not striate). While fine straight forceps could be used, we found curved forceps to





be a much more versatile tool for the task. A large standard pin (e.g. no. 4) bent at an obtuse angle (Fig. 4) provides an inexpensive tool, instead of a second pair of forceps, to help in holding the specimens or the wings during pinning and setting. It is important to use a pin that is not too fine because the point may catch and rip into the wings too easily.

**Setting triangles** (Fig. 5). Triangles are used to hold the wings in place once they are spread. They are made with a point punch (of the type commonly used for mounting small insects) from moderately thick, very smooth or glossy card and inserted no more than half way up on short pins. We use two sizes of triangles [7 mm long with pointed end (Fig. 17) and 10 mm long with truncate end (Figs. 10–12)] for different sizes of microlepidoptera. We mount them on pins no. 00 cut down to 1 cm in length (trimmed the same way as the minutens). Do not use minutens for mounting triangles because they are too fine to insert easily into the relatively thick card stock of the triangles. When mounting triangles, check that the side with rough edges (produced by the punch on the underside of the paper) is turned upwards (check with a magnifying lens if necessary). If this simple precaution is not taken, much damage to the wing scales will occur because of the rough edges of the triangles. As for minutens, a large supply of mounted triangles should be readied, pinned in shallow boxes. Triangles are re-used indefinitely or until they become loose on the supporting pins.

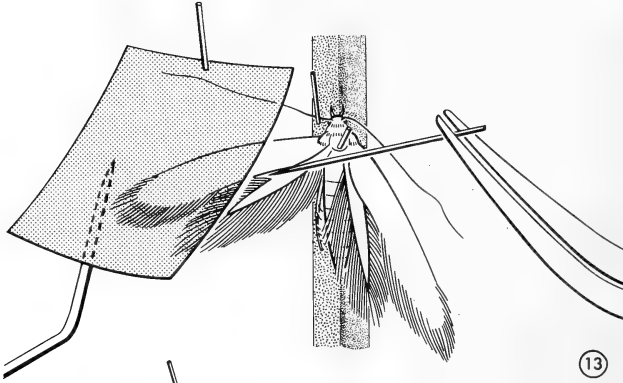
**Pinning pad.** White cotton fabric folded several times into a pad about 1 cm thick and 10 cm × 10 cm makes an ideal surface to pin microlepidoptera. The fabric must be as soft as possible. This surface prevents specimen compression when pinning and the fabric fibres tend to hook the moth claws, thus reducing slippage. Avoid paper towels of any kind, they are usually too rough. The thickness of the pad must be greater than the length of the minutens so that the pad does not have to be lifted up when pushing the minutens through the specimens.

**Humid container.** This serves to hold pinned specimens to prevent them from drying while they await setting. If this precaution is not taken, the smaller microlepidoptera will begin to dry in a mere few

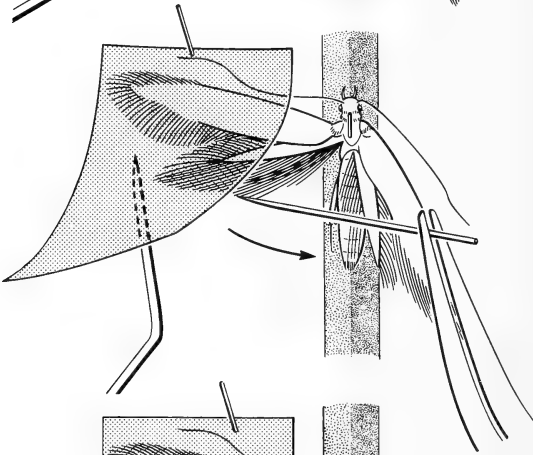
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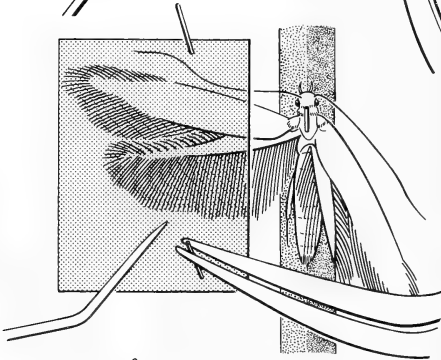
FIGS. 9–12. Setting with the point method. **9**, Inserting the specimen into the groove with the wings partly opened; **10**, Moving one set of wings forward with the point-holding pin; note the antenna held in position with a minuten; **11**, Setting the wing into position with the mounted point while holding it with the bent pin; **12**, Repeating the operation with the other side.



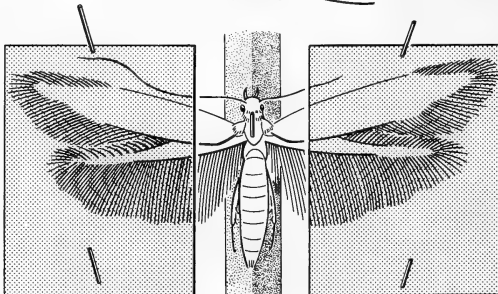
13



14



15



16

minutes in dry air and become difficult to spread by the time one gets to the last few of a batch. The container is simply made from a plastic petri dish or similar small plastic dish or box with a loosely fitting lid. The bottom of the dish is lined with wetted tissue or filter paper. A small plastazote pad serves to hold specimens. In very dry conditions, the inside of the lid may be *lightly* misted to increase ambient moisture in the container (too much moisture could drip on the specimens).

#### PINNING AND SETTING

For best results (and less eye strain) the pinning and setting operations should be done with magnifying lenses or under a low-power stereoscope (up to about  $5\times$ ).

Pour the freshly killed moths on the cotton pad and pin them. Insert the minuten through the center of the mesothorax (mesoscutum) or at the suture between the mesoscutum and mesoscutellum (the mesoscutellum is the roughly triangular or diamond-shaped area behind the center of the mesothorax). Try to keep the pin in line with the center of the thorax, otherwise the wing muscles may become transfixed, which renders spreading more difficult. To ensure that a specimen is squarely pinned, apply very slight pressure on its dorsum with the tip of the bent pin (or another curved forceps) to prevent the body from rolling sideways while the minuten is inserted into the mesothorax (Fig. 7). The minuten must be inserted far down so as to leave no more than about 2 mm protruding above the moth, enough to manipulate it comfortably with forceps (Fig. 8). Of course, the height of specimens with unusual structural modifications such as long palpi recurved over the body or thoracic crests should be adjusted appropriately in order to leave sufficient minuten length for the forceps; such specimens may require longer (untrimmed) minuten.

Place pinned specimens in the humid container. Prior to this, if one wishes, the wings may be partly opened by gently blowing on them from behind the moth with a slight puff of breath. Before proceeding with setting, another series of specimens is transferred to the killing tubes. Hence, there will be specimens ready for pinning when the first batch has been set. We usually proceed in batches of no more than 15–25 moths.

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←

FIGS. 13–16. Setting with the paper method. **13**, Moving one set of wings forward with a minuten while lifting the paper strip with the bent pin; note the minuten holding the antenna; **14**, Combing the fringe; arrow indicates direction of combing movement; the combing minuten touches the tip of the fringe lightly; **15**, Pinning the paper strip down to secure the wing into position; the minuten holding the antenna may be removed as it is usually no longer necessary; **16**, Set specimen.

Take specimens out of the humid container singly for setting. If the wings are still closed, gently blow on them from behind, then insert the specimen into the groove (Fig. 9). Lift the wings and partly push them forward with the tip of the closed curved forceps inserted beneath the wings. Tuck the legs into the groove. With a minuten position the antennae so that they form a widely obtuse V, holding them temporarily by placing minuten behind their base. If the fringes are matted, lift the wings a little and comb the fringes by brushing them with the tip of the triangle's pin in a movement going from the apex of the wings toward the body.

To fix the wings into position, we use two different procedures.

**(1) Points method (Figs. 10–12).** This method may be a bit faster than the paper method (see below). Although excellent, it sometimes gives slightly inferior results, and makes it more difficult to set the antennae properly.

Using a mounted triangle, bring one pair of wings forward by pushing on the hind margin of the forewing with the tip of the pin. Usually, if this movement is delicately executed, both wings will move together because of the coupling. Do not pierce the wings. While holding the wings into position with a slight pressure of the bent pin held in the other hand, put the triangle on top of the wings as close to the apex of the hindwing as possible and push it down sufficiently to immobilise the wings. The triangle must lie flat against the wing surface and must not be pressed down too strongly or it will leave a mark. It may be necessary to adjust the position of the hindwing slightly, which sometimes will be a little too far back or too far forward. One or more triangles may be added to better hold the wings of larger or broad-winged microlepidoptera or to prevent them from curling up.

Repeat the procedure for the other side. To prevent set specimens from hindering hand work over the spreading box surface, it is best to proceed in transverse rows instead of filling one groove after another.

For someone having difficulty using both hands simultaneously, the following variation may be applied: using a mounted triangle as outlined above, move a pair of wings only halfway forward then insert the triangle over the wings just sufficiently to prevent the wings from slipping back but ensuring that they can still be moved; with a minuten move the wings into their final position (the wings should stay in place) and with the forceps maintained closed, gently push down the top of the pin holding the triangle until the wings are flat. Positioning of the wings in this way may have to be done in several stages for some specimens. The other hand may hold the spreading box. With this variation, one can proceed by filling one groove after another if desired.

**(2) Paper method (Figs. 13–16).** The second procedure uses small

strips of thin, translucent setting paper and is essentially similar to the standard technique used to spread larger *Lepidoptera* on a normal setting board. The paper strips are held down with 0.20 minutens. This technique can yield the finest specimens because the entire surface of the wings is held flat, and the antennae can be set properly with ease. It is a little more cumbersome and may take a little more time depending on individual ability. In our own experience, however, it takes about the same amount of time as the triangle technique, if one has prepared and has ready the necessary materials, such as pre-cut pieces of setting paper and minutens.

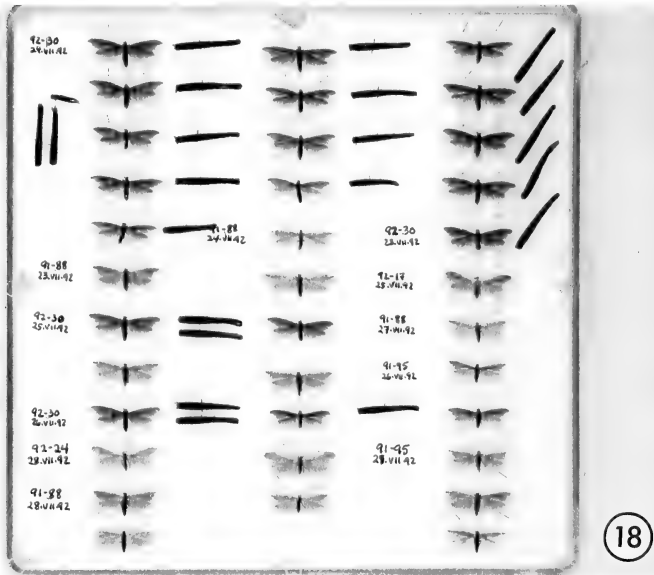
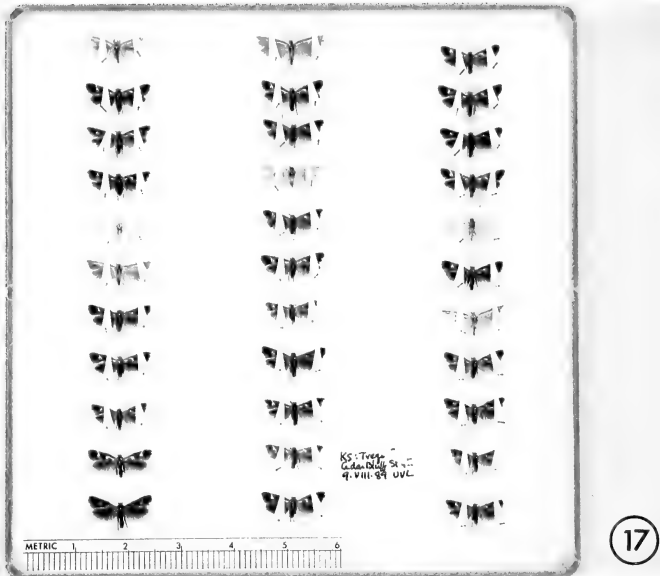
Cut many small pieces of setting paper, just long enough to cover the antennae and one set of wings, prior to spreading. For most microlepidoptera, the strips we use are about 1–1.5 cm long and about 5 mm wide. Four minutens are usually needed to spread one moth. For increased speed, sets of four paper-holding minutens may be pinned beside each groove of an entire row before the setting begins. When one row has been filled with specimens, another series of minutens is placed along the next row, and so on.

After pinning the moth and having set the antennae as described above, pick up a paper strip by stabbing it with a minuten and pin it just ahead of the antenna to cover the half-opened wings. Check that the curvature of the paper faces upward. With the bent no. 4 pin (or another pair of curved forceps) held in one hand, slightly lift the posterior end of the paper from beneath. With another minuten held with curved forceps in the other hand and working from behind the hind margin of the forewing, push the wings into position. When both wings are positioned, drop the paper strip, hold it down with the tip of the bent no. 4 and pin it behind the hindwing with a second minuten. Repeat on the other side.

Choosing the appropriate groove width will facilitate spreading. A groove too narrow will force the legs up and put pressure on the thorax, thus hindering wing movement. A groove too wide will result in either the specimen swinging on the pin when the wings are pushed on one side, or in an insufficient portion of the wing surface resting flat.

Before placing the specimen into the groove, the plastazote surface may be gently rubbed with the tip of the closed forceps to create a charge of static electricity which will help in spreading the wings. This is not necessary, however, if one is using the paper strip method, and it is not recommended with very small microlepidoptera such as nepiculids because the charge will be too strong and may push the wings up vertically.

With a fresh, fully relaxed moth and some practice, the whole operation of pinning and setting takes no more 30–60 seconds. With



FIGS. 17-18. Examples of filled spreading boxes. 17, Point-set specimens; 18, Paper-set specimens (larval cases beside reared specimens). Scale in cm.

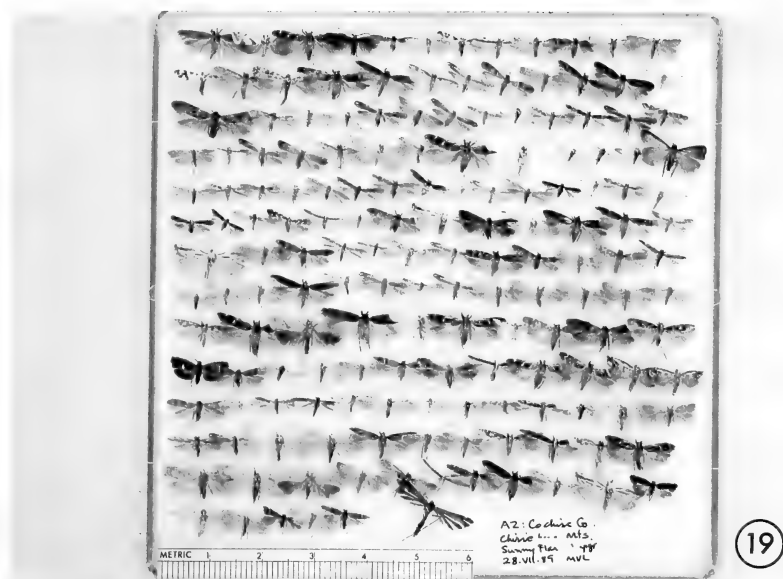


FIG. 19. Example of packed spreading box in which previously set and dry specimens are overlapped like shingles to conserve space. This 11 × 11 cm box contains 166 specimens.

practice, specimens can be set quite closely behind one another into the grooves to conserve space (Figs. 17–18).

Stunning prior to spreading is sometimes used, instead of killing, when time is short (Sokoloff 1980). If specimens are only anesthetized (stunned) prior to spreading, it is necessary to pin a small cotton swab imbibed with ammonia into the spreading box and close it for about 15–20 minutes to kill the moths. If the spreading box is made of polystyrene-base plastic, avoid ethyl acetate because it will dissolve the plastic. We do not use the stunning method because we find it inconvenient, especially in the field.

Label the specimens as usual and leave them in the spreading boxes in a dry place for at least two weeks, or preferably for as long as possible. If one does not provide enough time for the specimens to dry, the tips of some wings may curl up or droop. In humid regions, it is advisable to secure a few crystals of 4-chloro-m-cresol in the boxes to prevent molding. Once the moths are dry, full boxes should be sealed tightly with tape until ready for staging.

When in the field for an extended time and spreading boxes are in short supply, or to reduce the number of boxes being transported, space can be saved by removing specimens from the grooves after drying

and packing them somewhat like shingles (Fig. 19). Specimens are pinned slanted in transverse rows, with the left wings of a specimen partly overlapping the right wings of the preceding one. This allows for large quantities of specimens to be stored in little space. An entire collection of several thousands of microlepidoptera can be carried in this way in a handbag on a plane instead of being placed in regular baggage, thus maximizing the safety of specimens that may represent months of field work in a remote region.

Some authors have recommended heat-drying because, supposedly, moths that have been heat-dried will never have drooped wings (Amsel 1935). This is, however, a delicate and risky operation that must be done very carefully with *very low* heat (ca. no more than 40° C). We have tried drying on a few occasions and are rather weary of it. We have noticed that several microlepidoptera tend to become a little greasy when dried with heat (noticeable under magnification). Another problem is that the plastazote of the spreading boxes may warp slightly from being heated. We think that it is preferable to see some wing drooping occur later in the collection than risk damaging specimens in heat-drying. Wing drooping will be minimized or virtually eliminated if specimens are allowed to remain set in the spreading boxes for an extended period.

#### STAGING

To be placed in collections, dry minuten-pinned microlepidoptera must be mounted individually on small rectangular blocks, which are inserted on standard (# 3 or 4) insect pins. This is referred to as staging or double-mounting. Specimens should always be mounted *singly* on a block, complete with all necessary labels on the supporting pin, except perhaps in cases of mated pairs which may be staged together. It is very annoying to find two or more microlepidoptera belonging to different but superficially similar species that have been staged together with a single label; such specimens have to be remounted separately and new labels produced. Multiple mounts also increase the risk of misassociation of subsequently made genitalia slides.

**Staging blocks.** It is more efficient to prepare large quantities of blocks in advance. Traditionally, blocks have been cut from strips of polypore fungi (especially from birch bracket fungus). Normally it is easy to procure polypore strips from naturalist supply houses, but periodically they tend to become very difficult to obtain.

Plastazote provides a superior substitute. It is comparatively inexpensive, available in practically infinite supply, extremely regular in density, practically unalterable, and pest proof (we once had a supply of polypore strips heavily infested with ciid beetles). Plastazote allows



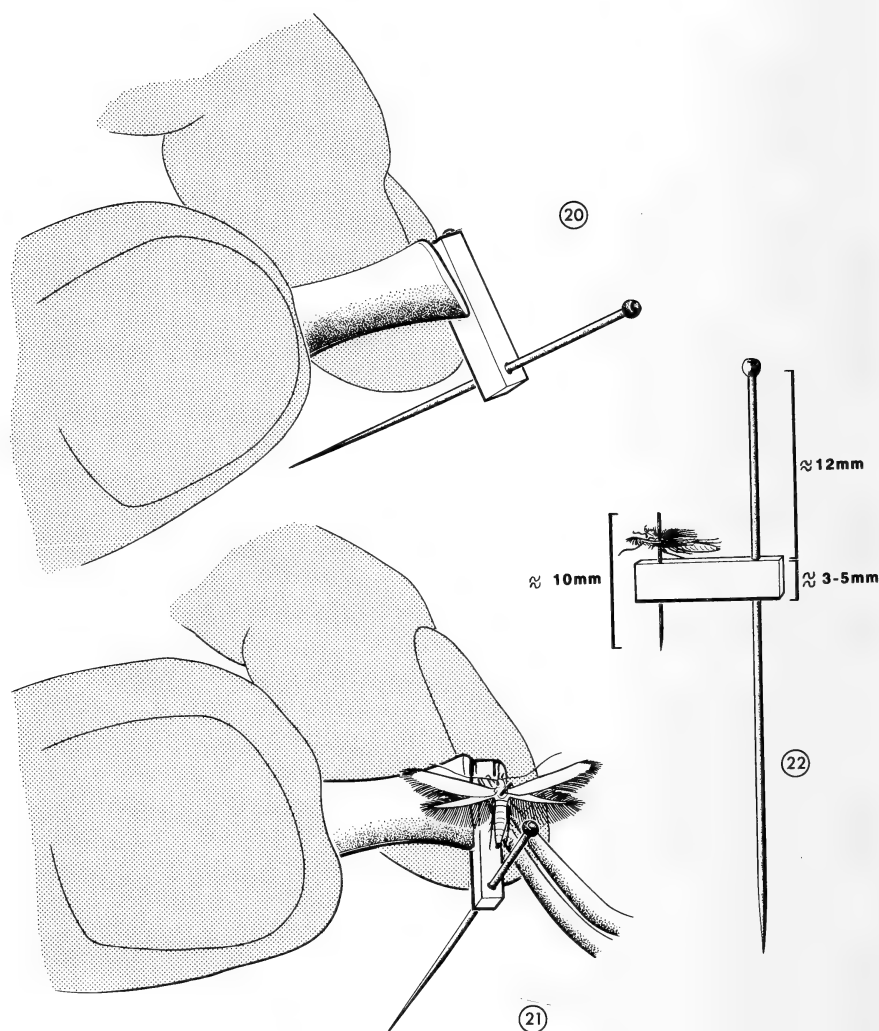
the finest minutenens to be inserted without effort and provides remarkable protection from shocks and vibrations. Other materials such as balsa, cork, and polystyrene-based foam ("styrofoam") should be avoided because they are either too hard to insert the minuten without risking damage or are not rubbery enough to hold firmly the pin and the minuten (the latter is a problem of balsa and polystyrene-based foams, on which minutenens frequently become loose). Blocks made of a silicon rubber compound are used by some but their durability is uncertain in insect drawers where they may be affected by fumigants; we have seen a set of such blocks that were about 15 years old and that exuded a greasy substance which seeped up the minutenens and coated the specimens. It is also harder to insert a minuten into silicon rubber, which is a springy material.

The length of the blocks varies with the size of the specimens. Ideally, we think that they should be about as long as the length of the moth from its head to the tip of its abdomen plus about 3 mm to provide space for the legs and the supporting pin. The width and height vary little and are from 2–3 mm (width) and from 2–4 mm (height). We recommend the use of as few sizes of blocks as necessary to maintain some uniformity to the collection. A cutting board with preset guides and mounted razor blade can be made to speed the cutting of large numbers of uniformly sized blocks. It is essential to mount the blocks on standard pins *prior* to double-mounting the moths. Staging blocks must be inserted up to a height that will leave adequate clearance between the specimen and the head of the supporting pin to allow for safe handling of the whole mount (Fig. 22); we recommend at least a 1 cm clearance.

**Staging procedure** (Figs. 20–21). To facilitate staging, use one pair of forceps with curved tips and another with broad, flattened tips.

With the flat-tip forceps, hold the pinned block in front of you. With the curved forceps, take the specimen by holding the minuten from beneath the specimen and insert slightly into the block. Check that the plane of the wings is perpendicular with the axis of the pin and adjust the inclination if necessary. Still grasping the minuten from beneath the specimen, pull it down into the block to the point where the venter of the moth is about 1 mm from the surface of the block.

Holding the minuten from beneath the specimen for insertion is especially critical if one is using polypore blocks. Polypore blocks vary markedly in hardness and pushing the minuten down while grasping it from above the specimen may cause the minuten to bend or spring, usually resulting in damage to the moth. Using plastazote blocks generally obviates this danger but grasping the minuten below the moth reduces the risk of damage in case of slippage of the forceps.



FIGS. 20-22. Staging or double-mounting. **20**, Holding with flat-tipped forceps a staging block mounted on a standard pin; **21**, Inserting the specimen on the stage, clamping the minuten from below the specimen; **22**, Staged specimen, showing good heights for safe subsequent handling.

It is important to insert the minuten as far down as possible, while not touching the stage, in order to secure the specimen (Fig. 22). Specimens protruding high on the block risk getting damaged in subsequent handling as much as those with overly long minutenus jutting high above the body.

## FINAL REMARKS

The techniques described above may seem laborious, but what takes many words to explain is actually executed in just a few seconds. With some practice, one can easily pin and set up to 30–40 microlepidoptera of fine quality per hour.

If there is no time or desire to fully spread all the moths that are collected, one may at least spread the wings partly and brush the fringes. Provisional spreading (Amsel 1935, Zimmerman 1978: pp. 48–ff, Nielsen 1980, Mikkola 1986), with subsequent relaxation and spreading if necessary or desired, is a good compromise where time is short such as during expeditions aiming at sampling as many specimens as possible. Damaged or rubbed specimens that may be worth collecting for some reason may be partially spread to save time.

Generally we do not use light traps and prefer to collect microlepidoptera at light on a sheet. Although light traps afford several advantages in sampling and are often necessary for surveys, we find that one is easily overwhelmed by the abundance of specimens so obtained, that a significant amount of time is necessary to sort the microlepidoptera from other Lepidoptera and insects, and that most specimens sustain a certain amount of rubbing and damage. If there is no time to relax and set trap-collected specimens right away, they should be placed on slightly damp cotton in tight containers and kept in a freezer.

Methods that involve killing the specimens immediately upon capturing them (as in light traps) and storing them for an indeterminate period of time (e.g. by freezing), generally necessitate some period of relaxation in a humid chamber before proper setting can be performed. Such specimens are usually not quite as easy to spread as freshly killed specimens and are not ideal for the point-setting technique described above, although satisfactory results can be obtained with adequate relaxation and using the paper-strip technique. Specimens that have dried unspread usually cannot be subsequently relaxed and spread. Some lepidopterists who have tried our technique complained that it was not quite as easy as we told them but, when pressed for details of how they proceeded, most conceded that they had killed their specimens upon collecting and spread them a little later without relaxation. We reiterate that working from fresh, live specimens killed just before setting is central to the ease and rapidity with which microlepidoptera can be set with the technique described here, and to obtaining high-quality specimens. Of course, some experience is necessary to achieve the best results; one is unlikely to obtain perfect microlepidoptera after attempting to set only a dozen specimens.

It is a truism that fine, well-prepared specimens are easier to identify.

This is particularly true for microlepidoptera, whose small size puts them at a disadvantage over the larger Lepidoptera when it comes to studying them (incidentally, lepidopterists facing space limitations to house their collection of macros should seriously consider taking up the collection of microlepidoptera!). Many well prepared microlepidoptera can be recognized at a glance. On the other hand, rubbed, damaged, or badly mounted specimens may be quite difficult to recognize, even to family, particularly if they are unspread.

Unavoidably, processing microlepidoptera soon after their collecting will take more time and seem more laborious than for larger Lepidoptera that are simply papered or pinned for subsequent setting. It can be argued, however, that the time involved strictly in spreading microlepidoptera is no more than for spreading macros; in fact spreading microlepidoptera is faster. The main difference is that one should do it right at the time of collecting for best results. The resulting quality of the specimens makes it well worth the effort.

#### ACKNOWLEDGMENTS

Several lepidopterists made suggestions and comments on our technique and on spreading microlepidoptera in general, and/or have encouraged us over the years to publish our method. In particular, we are indebted to Vitor Becker, Bengt Bengtsson, Don Davis, John De Benedictis, Michael Fibiger, John Grehan, Ron Hodges, Ole Karsholt, Eric Metzler, Kauri Mikkola, John Morton, Jerry Powell, Tony Roberts, Klaus Sattler, Dave Wagner, Monty Wood, and Don Wright. We thank Eric Metzler for making us aware of ammonium carbonate, and Cees Gielis for testing it under harsh field conditions. We thank Dave Moorehouse for his assistance in preparing the figures. Ole Karsholt, Jeff Cumming, Mike Sharkey, Kevin Tuck, and an anonymous reviewer, provided many useful comments on the manuscript.

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## CHECKLIST OF SOUTH DAKOTA BUTTERFLIES (HESPERIOIDEA AND PAPILIONOIDEA)

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**ABSTRACT.** This paper presents a list of 172 butterfly species (Hesperioidea and Papilionoidea) documented from South Dakota. The list was compiled from records of resident and non-resident collectors, published literature, and university collections. For each species all recorded counties and adult flight periods are given.

**Additional key words:** distributions, Great Plains.

This paper is the first comprehensive treatment of South Dakota's butterfly fauna. An early list of butterfly species by Truman (1896, 1897) covers an area near Volga, Brookings County. Many of Truman's specimens are deposited in the H. C. Severin Insect Collection at South Dakota State University. Other regional works include those for Siehe Hollow State Park in Marshall and Roberts counties (Masters 1975), and the Black Hills (Conway 1966). Papers treating only a species or group of species include Ferris (1969, 1976, 1981, 1983), Grey et al. (1963), McCabe (1981), Nordin (1967, 1968), and Scott and Stanford (1981). Many records for the western half of the state, west of the 100th meridian, are mapped by Stanford (Ferris & Brown 1981). Stanford and Opler (1993) reported butterfly species occurrences (county dot maps) for the western United States, including all of South Dakota.

South Dakota is known as the "land of infinite variety" because of the diversity of terrain, habitat, and climate. There is a general increase in elevation from 335 m in the southeast to 1035 m in the northwest; the highest point is Harney Peak (2209 m) in the Black Hills and the lowest is on the Minnesota River (293 m) in the northeast corner of the state. The state is mostly gently rolling grassland with the Missouri River dividing it from north to south into two nearly equal parts. The area east of the river is characterized by a glaciated topography with tall grass, low rolling hills, and many lakes and marshes. The western, semi-arid mixed grass prairie, portion of the state has deep valleys and broad upland flats and buttes. The Black Hills, on the extreme western edge of the state, may be regarded as an outpost of the Rocky Mountains. Mean annual precipitation ranges from 66 cm in the southeast and Black Hills, to less than 30.5 cm in the northwest.

One hundred seventy-two species of butterflies are known to occur in South Dakota. Of these, 132 are residents and the remainder are immigrants or strays. Other species undoubtedly will be added to this list as collecting continues. The author encourages anyone who can provide additional information to contact him.

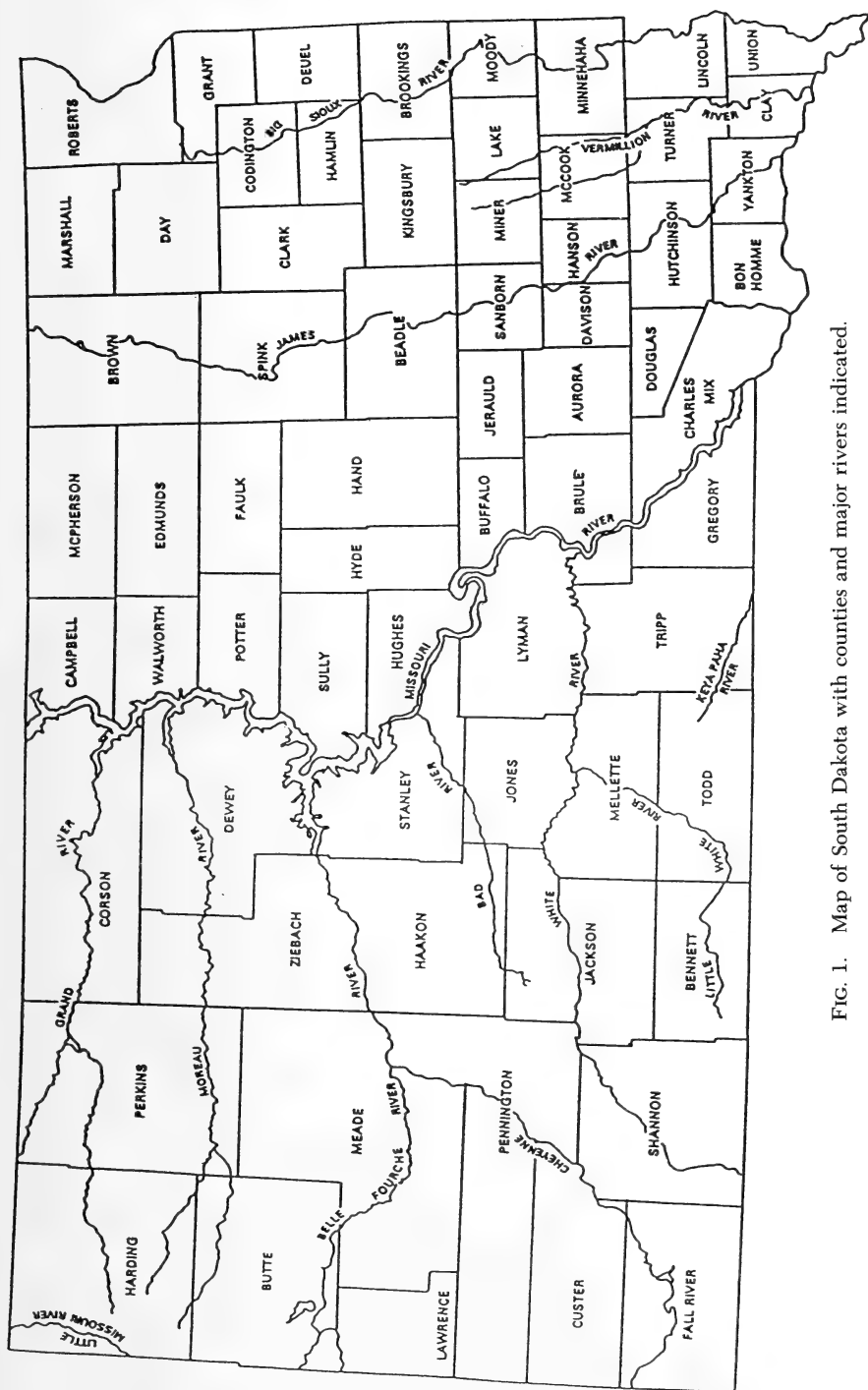


FIG. 1. Map of South Dakota with counties and major rivers indicated.

A "butterfly calendar," illustrating adult flight periods, was developed based on 6,500 South Dakota butterfly records (Table 1). Data were lacking for some species so approximations were made. The number of species occurring per each month is as follows:

Apr	May	Jun	Jul	Aug	Sep	Oct
20	76	137	131	93	53	17

More than 2,500 county records, tabulated through December 1993, are presented. This equates to an average of 39 species from each of South Dakota's 66 counties. County locations and names are shown in Fig. 1. The number of species known per county ranges from 11 for Edmunds County to 117 for Pennington County (Table 2). In general, the counties with the highest totals are those of the Black Hills which is a reflection of a greater sampling effort combined with a broad diversity of habitats. The counties with the fewest reported species are generally highly agricultural or have not been surveyed thoroughly. No species has been documented for all South Dakota counties; however, five species have been recorded for more than 60 of the 66 counties: *Pieris rapae*, *Colias eurytheme*, *Colias philodice*, *Lycaeides melissa*, and *Cercyonis pegala*. Twenty-seven counties have fewer than 30 species recorded. South Dakota's total of 172 species ranks fourth among its bordering western Great Plains states: Wyoming—210, Nebraska—197, Montana—187, and North Dakota—143 (Stanford & Opler 1993).

Data for county records were obtained from the following sources:

- (1) The collections at South Dakota State University, Brookings; University of South Dakota, Vermillion; Northern State University, Aberdeen; and North Dakota State University, Fargo.
- (2) Private collections of Gerald Fauske, Fargo, N.D., who collected primarily in the vicinity of Sioux Falls; Bruce K. Harris, Clear Lake; Abran and Joseph Kean, Pierre; John S. Nordin, formerly of Webster, who collected extensively during 1965 to 1971; and the personal collection of the author.
- (3) A review of the literature, including Season Summaries of The Lepidopterists' Society (1976–1993).
- (4) South Dakota collection records provided by non-resident collectors.

Taxonomy and nomenclature follow *A Catalogue/Checklist of the Butterflies of America North of Mexico* (Miller & Brown 1981) and its supplement (Ferris 1989).

The following species and subspecies have type localities designated in South Dakota:

*Erynnis persius fredericki*—"Spearfish Canyon, Lawrence Co., South Dakota."



TABLE 1. Summary of butterfly flight periods in South Dakota and general comments on each species. Each mark represents on the average a ten day period. The markings indicate: (.) non flight period, (-) few or worn specimens and (\*) fresh specimens.

Species	May	Jun	Jul	Aug	Sep	Oct	Range of extreme dates	Comments
<i>Epergyreus c. clarus</i>	..	***	*--	---	...	...	May 24-Aug 22	statewide
<i>Thorubus pylades</i>	..	***	---	...	...	...	May 23-Jul 25	western ½ SD, univoltine
<i>Staphylus hayhurstii</i>			one record				Sep 08	Yankton Co., stray?
<i>Erynnis icelus</i>		four records, one date					Jun 24	Black Hills
<i>Erynnis b. brizo</i>		no dates available						extreme eastern SD, stray?
<i>Erynnis j. juvenalis</i>	*	two records, only one date					May 25-Jun 23	scattered statewide, uncommon
<i>Erynnis horatius</i>	*						Aug 10	extreme eastern SD
<i>Erynnis martialis</i>	..	*	...	...	...	...	May 25-Jul 10	northern Black Hills
<i>Erynnis afrauentis</i>	..	***	---	...	...	...	Jun 23-Jul 30	western ½ SD
<i>Erynnis persius fredericki</i>	..	...	---	...	...	...	May 03-Jul 13	western ½ SD
<i>Pyrgus scriptura</i>	..	...	---	...	---	---	May 02-Jul 11	statewide, uncommon
<i>Pyrgus communis</i>	..	*	---	***	---	---	May 24-Oct 15	statewide, common, bivoltine
<i>Pholisora catullus</i>	..	*	---	*	...	...	May 07-Aug 10	statewide, bivoltine
<i>Ancyloxypha numitor</i>	...	---	***	*	---	---	Jun 06-Sep 03	statewide, near water
<i>Oarisma poweshiek</i>	...	*	---	...	...	...	Jul 01-Jul 14	northeast SD, near wetlands
<i>Oarisma garita</i>	...	..	---	...	...	...	Jun 13-Jul 08	western ½ SD
<i>Hylephila p. phyleus</i>	**	---	one record				Oct 07	extreme southeast SD, stray?
<i>Yvretta rhesus</i>	...	...	...	...	...	...	May 07-Jul 10	western ½ SD
<i>Hesperia u. uncus</i>	...	*	**	---	---	---	Jun 21-Sep 04	scattered statewide
<i>Hesperia juba</i>		one record					Jun 13	Lawrence Co., stray?
<i>Hesperia comma assiniboia</i>	...	...	...	*	...	...	Aug 21-Sep 04	statewide, uncommon
<i>Hesperia ottoe</i>	...	*	---	---	...	...	Jun 23-Jul 30	statewide, uncommon, native prairie
<i>Hesperia leonardus pawnee</i>	...	...	...	*	...	...	Aug 13-Sep 09	statewide
<i>Hesperia p. pahaska</i>	..	**	---	...	...	...	May 31-Jul 10	western ½ SD
<i>Hesperia dacotae</i>	...	..	*	...	...	...	Jun 30-Jul 11	northeast SD, rare, native prairie
<i>Hesperia nevada</i>	...	one record					Jul 07	Pennington Co., stray?
<i>Polites peckius</i>	...	**	*	---	...	...	Jun 07-Aug 31	statewide
<i>Polites themistocles</i>	..	***	*	---	...	...	May 28-Aug 23	statewide, common
<i>Polites origenes rhena</i>	..	***	---	---	...	...	May 31-Jul 30	northeast and western SD
<i>Polites mystic dacotah</i>	...	**	*	---	...	...	Jun 06-Aug 13	statewide, wet areas

TABLE 1. Continued.

Species	May	Jun	Jul	Aug	Sep	Oct	Range of extreme dates	Comments
<i>Wallengrenia egeremet</i>	...	..	*--	...	...	...	Jul 01-Jul 09	extreme eastern SD, uncommon
<i>Pompeius verna</i>	...	**	..	...	...	...	Jun 21-Jul 18	southeast SD, rare
<i>Atalopedes c. campestris</i>	...	**	*--	..**	...	...	Jun 15-Oct 10	statewide, regular southern migrant
<i>Atrytone arozos iowa</i>	...	..	*	...	...	...	Jun 25-Jul 26	statewide, uncommon, native prairie
<i>Atrytone logan lagus</i>	..*	**	---	...	...	...	May 26-Jul 29	statewide
<i>Ochlodes sylvanoides napa</i>	...	..	...	*--	...	...	Jun 24-Sep 04	northern Black Hills
<i>Poanes m. massasoit</i>	...	two records,	...	...	...	...	Jun 06	northeast SD, rare
<i>Poanes h. hobomok</i>	..*	**	---	...	...	...	May 26-Jul 25	statewide
<i>Poanes zabulon</i>	...	one record	...	...	...	...	Jun 28	Brule Co., stray
<i>Poanes taxiles</i>	...	..*	*--	...	...	...	Jun 25-Jul 16	Black Hills
<i>Poanes v. viator</i>	...	..*	*--	...	...	...	Jul 03-Jul 08	northeast SD, near wetlands, local
<i>Euphyes vestris kiawah</i>	...	..*	---	...	...	...	Jun 18-Aug 15	statewide, uncommon
<i>Atrytonopsis hianna</i>	..*	---	---	...	...	...	May 24-Jul 04	statewide, scattered, dry hillsides
<i>Amblyscirtes simius</i>	..*	---	---	...	...	...	May 31-Jul 08	Black Hills, uncommon
<i>Amblyscirtes oslari</i>	..*	---	---	...	...	...	May 24-Jun 26	western 1/2 SD
<i>Amblyscirtes vitalis</i>	..**	---	---	...	...	...	May 07-Aug 30	statewide, univoltine
<i>Lerodea eufala</i>	three records,	...	...	...	...	...	Jun 25	Minnehaha & Day Cos., southern migrant
<i>Megathymus streckeri leussleri</i>	..*	**	---	...	...	...	May 24-Jul 08	western 1/2 SD, near yucca
<i>Parnassius phoebus sayii</i>	...	**	---	...	...	...	Jun 06-Jul 17	Black Hills, near sedum
<i>Battus p. philenor</i>	no dates available	one record,	...	...	...	...	Apr 30-Sep 29	stray, Brookings and Minnehaha Cos.
<i>Eurytides marcellus</i>	**	---	---	---	---	...	May 03-Aug 26	stray, Minnehaha Co.
<i>Papilio polyxenes asterius</i>	*--	...	---	---	...	...	Apr 24-Aug 05	statewide, rare western 1/2 SD
<i>Papilio b. baivardi</i>	**	---	---	---	...	...	Jun 06-Sep 15	western 1/2 SD, uncommon
<i>Papilio zelicaon nitra</i>	...	**	---	---	...	...	Jun 10-Sep 01	Black Hills, rare
<i>Papilio i. indra</i>	...	..	...	**	---	...	Apr 29-Sep 04	resident, extreme southeast SD
<i>Heracides crespontes</i>	*--	---	---	---	---	...	Jun 05-Jul 21	eastern 1/2 SD, bivoltine
<i>Pterourus g. glaucus</i>	...	---	---	---	...	...	Jul 07-Jul 24	Black Hills and extreme northeast SD
<i>Pterourus canadensis</i>	...	---	---	---	...	...	May 22-Aug 05	Black Hills, rare
<i>Pterourus r. rutulus</i>	..*	**	---	---	...	...	Jun 16-Jul 20	western 1/2 SD
<i>Pterourus multicaudatus</i>	...	..	---	---	...	...		northern Black Hills, rare
<i>Pterourus eurymedon</i>	...	**	---	---	...	...		

TABLE 1. Continued.

Species	May	Jun	Jul	Aug	Sep	Oct	Range of extreme dates	Comments
<i>Pterourus t. troilus</i>	...	two records, no dates						southern migrant, rare
<i>Neophasia m. menapia</i>	...	...	...	**	---	...	Aug 08-Sep 18	Black Hills
<i>Pontia sisymbrii nordini</i>	***	---	...	...	...	...	Apr 16-Jun 09	Black Hills and Harding Co.
<i>Pontia protodice</i>	---	*	...	***	---	---	Mar 03-Oct 06	statewide, common
<i>Pontia o. occidentalis</i>	---	*	---	---	---	...	May 03-Sep 04	mostly western $\frac{2}{3}$ SD
<i>Pieris napi oleracea</i>	---	three fresh specimens				...	Jul 05	Marshall and Roberts Cos., stray
<i>Pieris napi mcduffnoughi</i>	---	one record				...	Jun 23	Lawrence Co., stray
<i>Pieris rapae</i>	*	***	***	***	*	---	Apr 16-Oct 06	statewide
<i>Ascia monuste</i>	---	one record				...	May 26	Brown Co., southern migrant
<i>Euchloe ausonides palaeoreios</i>	---	...	...	...	...	...	May 06-Jul 21	Black Hills
<i>Euchloe olympia</i>	***	...	...	...	...	...	Apr 25-Jun 11	statewide, univoltine
<i>Anthocharis sara julia</i>	---	one record				...	Jun 23	Lawrence Co., migrant
<i>Colias philodice</i>	---	***	***	***	*	---	Apr 13-Dec 09	statewide, multivoltine
<i>Colias eurhytheme</i>	---	***	***	***	*	---	May 10-Oct 09	statewide, multivoltine
<i>Colias a. alexandra</i>	---	---	---	---	---	---	May 24-Sep 03	Black Hills & Jackson Co., uncommon
<i>Colias alexandra krauthii</i>	...	*	*	---	---	...	Jun 23-Jul 27	Black Hills
<i>Zerene c. cesonia</i>	---	---	*	---	---	...	May 10-Aug 30	mostly southeast SD, southern migrant
<i>Phoebis sennae eubele</i>	...	two records, one date				...	Aug 15-Sep 26	southeast SD, rare southern migrant
<i>Phoebis a. agatithe</i>	---	one record, no date				...	May 21	Brookings and Minnehaha Cos., migrant
<i>Eurema d. daira</i>	---	...	---	...	...	...	May 10-Jul 27	Minnehaha Co., southern migrant
<i>Eurema mexicana</i>	---	...	---	...	...	...	May 28-Oct 01	eastern $\frac{1}{2}$ SD, regular migrant
<i>Eurema l. lisa</i>	---	...	---	---	---	---	May 11-Oct 27	Minnehaha Co., rare southern migrant
<i>Eurema nicippe</i>	---	two records, no dates				---		regular southern migrant
<i>Nathalis iole</i>	---	---	---	---	---	---		Marshall Co., stray?
<i>Feniseca t. tarquinius</i>	---	one record, no date				---	Jun 01	Jackson Co., stray?
<i>Lycæna phlaeas americana</i>	---	three records, one date				---	Jun 11-Jul 29	statewide, univoltine
<i>Gaetides xanthoides dione</i>	...	*	---	---	---	...	Jun 04-Sep 06	statewide, bivoltine
<i>Hylolycaena hyllus</i>	...	---	*	---	---	...	Jun 20-Jun 27	western $\frac{1}{4}$ , rare, univoltine
<i>Chalcidia rubida longi</i>	...	---	---	---	---	...	May 18-Sep 18	statewide, multivoltine
<i>Epidemia helleoides</i>	---	*	---	---	---	...	Jun 16-Aug 29	statewide, univoltine
<i>Harknclenus t. titus</i>	...	---	---	---	---	...		

TABLE 1. Continued.

Species	May	Jun	Jul	Aug	Sep	Oct	Range of extreme dates	Comments
<i>Satyrium acadicum montanensis</i>	...	...	*—	—	...	...	Jun 18-Aug 01	widely scattered statewide, univoltine
<i>Satyrium edwardsi</i>	...	...	one record	—	...	...	Jul 05	Roberts Co.
<i>Satyrium calanus falacer</i>	...	...	—	—	...	...	Jun 18-Aug 18	widely scattered statewide
<i>Satyrium caryaeorum</i>	...	...	one record	—	...	...	Jun 18	Lawrence Co.
<i>Satyrium liparops</i>	...	*	—	...	...	...	Jun 16-Jul 20	scattered statewide, rare
<i>Mitoura s. sita</i>	...	*	—	—	...	...	May 24-Aug 05	western ½ SD, univoltine
<i>Mitoura g. grynea</i>	—	—	one record	—	...	...	Jul 30	Union Co., stray?
<i>Incisalia angustinus iroides</i>	—	—	...	...	...	...	May 03-Jun 22	Black Hills
<i>Incisalia polia obscura</i>	—	—	...	...	...	...	May 02-Jun 25	Black Hills, very local
<i>Incisalia e. eryphon</i>	—	—	—	—	...	...	Apr 30-Jun 23	Black Hills, Harding and Todd Cos.
<i>Strymon melinus atrofasciatus</i>	—	—	—	—	—	...	Apr 30-Sep 29	statewide, multivoltine
<i>Leptotes marina</i>	—	two records, one date	—	—	—	...	Aug 02	Minnehaha and Pennington Cos., rare
<i>Hemiargus isola alce</i>	...	—	—	—	—	—	May 25-Oct 01	statewide, migrant, multivoltine
<i>Everes c. comyntas</i>	...	—	—	—	—	...	May 27-Sep 09	statewide, multivoltine
<i>Everes amyntula valeriae</i>	—	*	—	—	...	...	Apr 28-Aug 01	Black Hills
<i>Celastrina argiolus</i>	—	***	—	—	—	...	Apr 05-Sep 02	statewide, multivoltine
<i>Glauropsyche piasus daunia</i>	...	—	...	...	...	...	Jun 02-Jun 25	Black Hills and Harding Co.
<i>Glauropsyche lygdamus oro</i>	...	*	...	...	...	...	Apr 14-Jul 19	western ½ and northeast SD
<i>Lycæides m. melissa</i>	...	***	***	**	—	—	May 16-Oct 07	statewide, common, bivoltine
<i>Plebejus s. saepiolus</i>	...	***	—	...	...	...	May 31-Jul 27	Black Hills and Harding Co.
<i>Icaricia icarioides lycea</i>	...	**	—	—	...	...	Jun 02-Aug 14	Black Hills and Harding Co.
<i>Icaricia shasta minnehaha</i>	...	—	one record	—	...	...	Jun 26	Black Hills, rare
<i>Icaricia acmon lutzii</i>	*	...	...	...	...	...	May 24-Aug 02	western ½ and northeast SD
<i>Agricides r. rusticus</i>	...	*	—	...	...	...	Jun 03-Jul 09	Black Hills, very local, univoltine
<i>Apodemia m. mormo</i>	...	one record, no date	—	—	—	—	—	Pennington Co., stray?
<i>Libytheana b. bachmanii</i>	...	...	...	...	...	...	Jul 17-Oct 07	eastern ¼ SD, southern migrant
<i>Agraulis vanillae incarnata</i>	...	three records, one date	—	—	—	—	Jul 22	rare, stray
<i>Euptoietta claudia</i>	—	***	*	*	—	—	May 09-Oct 18	statewide, regular migrant
<i>Speyeria cybele</i>	...	***	—	—	—	...	Jun 06-Sep 02	statewide, univoltine, forest margins
<i>Speyeria aphrodite</i>	...	*	—	—	...	...	Jun 08-Aug 14	statewide, univoltine
<i>Speyeria idalia</i>	...	*	—	—	—	...	Jun 12-Sep 14	statewide, except NW corner, prairies

TABLE 1. Continued.

Species	May	Jun	Jul	Aug	Sep	Oct	Range of extreme dates	Comments
<i>Speyeria edwardsii</i>	..	***	---	---	---	...	May 24-Sep 18	western 1/2 SD, univoltine
<i>Speyeria coronis</i>	...	..	---	...	...	...	Jun 16-Jul 27	Black Hills & Harding Co., uncommon
<i>Speyeria zerene garretti</i>	...	..	---	...	...	...	Jun 23-Aug 05	Black Hills & Harding Co., uncommon
<i>Speyeria callippe calgariana</i>	...	..*	*	...	...	...	Jun 06-Jul 14	scattered western 1/2 SD, univoltine
<i>Speyeria atlantis</i>	...	..	***	---	...	...	Jun 18-Aug 15	Black Hills and Shannon Co.
<i>Speyeria mormonia eurynome</i>	...	..*	*	...	...	...	Jun 22-Jul 28	Black Hills and Shannon Co.
<i>Clossiana selene myrina</i>	...	..*	*	---	...	...	Jun 15-Aug 15	northeast SD, wet areas
<i>Clossiana selene nebraskensis</i>	...	..	---	...	...	...	May 29-Jul 23	extreme south central SD, wet areas
<i>Clossiana bellona toddi</i>	---	---	---	...	...	...	Jun 09-Jul 27	Black Hills
<i>Charidryas gorgone carlota</i>	---	---	*	---	---	...	May 08-Sep 02	eastern 1/4 SD, wet areas
<i>Charidryas n. nycteis</i>	---	*	*	---	---	...	Apr 10-Sep 05	statewide, bivoltine
<i>Charidryas acastus</i>	..	---	...	..	...	...	Jun 08-Aug 18	statewide
<i>Anthanasia t. texana</i>	---	---	one record	...	...	...	May 19-Aug 24	scattered western 1/2 SD, bivoltine
<i>Phytodes t. tharos</i>	---	***	***	**	---	---	Jul 07	Roberts Co., rare migrant
<i>Phytodes pascoensis</i>	...	*	*	...	...	...	Apr 26-Oct 09	statewide, multivoltine
<i>Phytodes batesii</i>	...	*	---	...	...	...	Jun 16-Jul 14	northeast and western SD, univoltine
<i>Phytodes pratensis camillus</i>	...	...	---	...	...	...	Jun 08-Aug 15	Black Hills, univoltine
<i>Phytodes pallidus barnesi</i>	..	...	---	...	...	...	Jul 08-Jul 27	Lawrence and Fall River Cos., uncommon
<i>Euphydryas anicia bernadetta</i>	---	*	---	...	...	...	May 25-Jul 08	Black Hills, uncommon
<i>Polygonia interrogatoria</i>	..	..*	***	...	...	...	May 08-Jun 25	western 1/4 SD, univoltine
<i>Polygonia comma</i>	---	---	***	***	---	---	May 28-Oct 01	statewide, rare western 1/2 SD
<i>Polygonia satyrus</i>	---	three records, one date	---	---	---	---	Apr 24-Oct 07	eastern 1/2 SD, near woods
<i>Polygonia faunus</i>	---	---	---	---	...	...	Aug 09	Black Hills, uncommon
<i>Polygonia zephyrus</i>	---	*	*	---	...	...	Apr 26-Aug 18	Black Hills, univoltine
<i>Polygonia p. prognie</i>	..	---	**	---	---	...	Apr 23-Sep 18	Black Hills
<i>Nymphalis vaualbum j-album</i>	..	..	*	---	---	...	Apr 30-Sep 24	statewide, scattered, near woods
<i>Nymphalis c. californica</i>	---	two records, no dates	---	---	---	...	May 05-Sep 13	Black Hills, northeast SD, migrant western migrant
<i>Nymphalis a. antiopa</i>	---	---	**	---	**	---	Mar 13-Oct 10	statewide, univoltine
<i>Aglais m. milberti</i>	---	*	*	---	*	---	Apr 09-Sep 27	statewide, common Black Hills
<i>Vanessa virginiensis</i>	..	---	---	..	...	...	May 30-Aug 01	statewide, uncommon

TABLE 1. Continued.

Species	May	Jun	Jul	Aug	Sep	Oct	Range of extreme dates	Comments
<i>Vanessa cardui</i>	---	---	---	**	---	...	Mar 31-Sep 22	statewide, large migration '83, '91, '92
<i>Vanessa annabella</i>	...	---	---	...	...	...	Jul 03-Jul 28	Black Hills, western migrant, rare
<i>Vanessa atalanta rubria</i>	---	---	*	**	---	...	Apr 30-Sep 18	statewide, common migrant
<i>Junonia coenia</i>	...	---	---	---	---	---	Jun 30-Oct 15	eastern 1/2 SD, southern migrant
<i>Basilarchia a. arthemis</i>	...	---	**	---	...	...	Jun 29-Aug 14	northeast SD, univoltine
<i>B. arthemis rubrofasciata</i>	...	---	*	---	...	...	Jun 16-Jul 14	northeast SD, univoltine
<i>B. arthemis astyanax</i>	...	*	---	**	---	...	Jun 07-Sep 09	eastern 1/2 SD, bivoltine
<i>B. a. archippus</i>	...	*	*	**	---	...	Jun 06-Sep 17	statewide, except northwest SD
<i>B. weidemeyerii oberfoelli</i>	...	*	*	---	...	...	Jun 06-Aug 15	western 1/3 SD, univoltine
<i>Mestra amymone</i>	...	one record	no date	---	---	---	---	Brookings Co., southern migrant
<i>Anaea andria</i>	...	...	---	---	---	...	Apr 30-Sep 02	southcentral SD, southern migrant
<i>Asterocampa c. celtis</i>	...	**	---	**	---	...	Jun 04-Sep 02	statewide except northwest SD
<i>Asterocampa c. clyton</i>	...	---	---	---	---	...	Jul 19-Aug 30	eastern 1/4, rare, univoltine
<i>Enodia anthedon</i>	...	*	*	---	---	...	Jun 16-Aug 24	eastern 1/4 SD, uncommon, wooded areas
<i>Satyrodes eurydice</i>	...	---	---	---	---	...	Jun 23-Aug 10	eastern 3/4 SD, near wetlands
<i>Megisto c. cymela</i>	...	*	*	---	---	...	Jun 12-Jul 31	statewide, wooded areas, univoltine
<i>Coenonympha tullia</i>	...	*	*	---	---	...	May 16-Aug 18	statewide, common, prairies
<i>Cercyonis pegala</i>	...	***	***	**	---	...	Jun 16-Sep 09	statewide, common, univoltine
<i>Cercyonis m. meadii</i>	...	*	---	*	---	...	Aug 01-Aug 19	Black Hills & Harding Co., uncommon
<i>Cercyonis oetus charon</i>	...	---	---	---	---	...	Jun 25-Aug 18	western 1/4 SD, uncommon, univoltine
<i>Neominois r. ridingsii</i>	...	---	*	---	---	...	Jun 17	Pennington Co., rare
<i>Oeneis c. chryxus</i>	...	two records, one date	---	---	---	...	---	Pennington Co.
<i>Oeneis uhleri</i>	*	one record, no date	---	---	---	...	May 10-Jul 17	western 1/4 & northeastern SD, prairies
<i>Danaus plexippus</i>	---	**	---	---	**	---	May 13-Oct 02	statewide, regular migrant

TABLE 2. Number of butterfly species documented for South Dakota counties. Counties are listed alphabetically.

Aurora	12	Hyde	22
Beadle	15	Jackson	40
Bennett	38	Jerauld	17
Bon Homme	12	Jones	31
Brookings	81	Kingsbury	22
Brown	33	Lake	23
Brule	46	Lawrence	115
Buffalo	15	Lincoln	35
Butte	33	Lyman	37
Campbell	15	McCook	23
Charles Mix	38	McPherson	39
Clark	16	Marshall	55
Clay	42	Meade	74
Codington	37	Mellette	38
Corson	30	Miner	15
Custer	106	Minnehaha	71
Davison	30	Moody	23
Day	77	Pennington	117
Deuel	52	Perkins	32
Dewey	21	Potter	29
Douglas	20	Roberts	64
Edmunds	11	Sanborn	21
Fall River	87	Shannon	43
Faulk	20	Spink	18
Grant	34	Stanley	51
Gregory	30	Sully	33
Haakon	24	Todd	46
Hamlin	25	Tripp	47
Hand	19	Turner	30
Hanson	17	Union	49
Harding	75	Walworth	26
Hughes	55	Yankton	49
Hutchinson	23	Ziebach	26

*Hesperia dacotae*—"Volga, South Dakota and Grinnell, Iowa."

*Euchloe ausonides palaeoreios*—"Spearfish Canyon, Lawrence Co., South Dakota."

*Colias alexandra krauthii*—"Black Hills, 12 mi. W. of Custer, Custer Co., South Dakota."

*Everes amyntula valeriae*—"Lead, South Dakota."

*Speyeria atlantis lurana*—"Harney Peak, Black Hills, South Dakota."

## COUNTY RECORDS OF SOUTH DAKOTA BUTTERFLIES

### Superfamily Hesperioidea

#### Family HesperIIDae

1. *Epargyreus clarus clarus* (Cramer)—Brookings, Brule, Clay, Custer, Davison, Day, Deuel, Dewey, Fall River, Hand, Harding, Hughes, Lake, Lawrence, Meade, Mellette, Minnehaha, Pennington, Roberts, Shannon, Stanley, Union.

2. *Thorybes pylades* (Scudder)—Custer, Fall River, Harding, Lawrence, Lincoln, Lyman, Mellette, Pennington, Roberts, Yankton.
3. *Staphylus hayhurstii* (W. H. Edwards)—Yankton.
4. *Erynnis icelus* (Scudder and Burgess)—Custer, Lawrence, Pennington.
5. *Erynnis brizo brizo* (Boisduval and Le Conte)—Brookings, Minnehaha.
6. *Erynnis juvenalis juvenalis* (Fabricius)—Brookings, Charles Mix, Custer, Lawrence, Meade, Mellette, Pennington, Roberts, Todd.
7. *Erynnis horatius* (Scudder and Burgess)—Brookings, Day, Yankton.
8. *Erynnis martialis* (Scudder)—Lawrence.
9. *Erynnis afranius* (Lintner)—Butte, Custer, Fall River, Harding, Lawrence, Meade, Pennington, Shannon, Ziebach.
10. *Erynnis persius fredericki* H. A. Freeman—Custer, Harding, Lawrence, Meade, Pennington, Perkins.
11. *Pyrgus scriptura* (Boisduval)—Custer, Fall River, Jackson.
12. *Pyrgus communis* (Grote)—Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clay, Codington, Corson, Custer, Davison, Day, Fall River, Grant, Gregory, Haakon, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Lake, Lawrence, Lincoln, Lyman, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Pennington, Potter, Roberts, Sanborn, Shannon, Stanley, Sully, Todd, Tripp, Union, Walworth, Yankton.
13. *Pholisora catullus* (Fabricius)—Bennett, Brookings, Brule, Butte, Charles Mix, Clay, Codington, Corson, Custer, Davison, Day, Dewey, Fall River, Faulk, Gregory, Haakon, Hanson, Harding, Hughes, Hutchinson, Jackson, Jones, Lawrence, McPherson, Meade, Mellette, Minnehaha, Pennington, Potter, Sanborn, Shannon, Stanley, Sully, Todd, Tripp, Turner, Yankton.
14. *Ancyloxypha numitor* (Fabricius)—Bennett, Brookings, Clark, Clay, Codington, Day, Deuel, Fall River, Grant, Hamlin, Hughes, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, McCook, Minnehaha, Pennington, Roberts, Shannon, Stanley, Walworth, Yankton.
15. *Oarisma powesheik* (Parker)—Brookings, Brown, Codington, Day, Deuel, Grant, Hamlin, Marshall, Roberts.
16. *Oarisma garita* (Reakirt)—Butte, Custer, Fall River, Harding, Lawrence, Meade, Pennington.
17. *Hylephila phyleus phyleus* (Drury)—Clay.
18. *Yvretta rhesus* (W. H. Edwards)—Bennett, Corson, Custer, Fall River, Harding, Jackson, Perkins.
19. *Hesperia uncas uncas* W. H. Edwards—Brookings, Codington, Custer, Day, Deuel, Fall River, Harding, Hughes, Jackson, Lawrence, McPherson, Meade, Pennington, Perkins, Potter, Stanley, Sully, Todd, Tripp.
20. *Hesperia juba* (Scudder)—Lawrence.
21. *Hesperia comma assiniboia* (Lyman)—Bennett, Custer, Day, Fall River, Harding, Lawrence, Marshall, McPherson, Pennington.
22. *Hesperia ottoe* W. H. Edwards—Brookings, Corson, Day, Deuel, Fall River, Harding, Lawrence, Pennington, Tripp, Union, Ziebach.
23. *Hesperia leonardus pawnee* Dodge—Bennett, Brookings, Butte, Custer, Day, Fall River, Harding, Hughes, Jackson, Lawrence, Marshall, Meade, Mellette, Pennington, Perkins, Roberts, Shannon, Stanley, Tripp, Union.
24. *Hesperia pahaska pahaska* (Leussler)—Custer, Fall River, Harding, Lawrence, Pennington, Ziebach.
25. *Hesperia dactotae* (Skinner)—Brookings, Brown, Codington, Day, Deuel, Grant, Hamlin, Marshall, McPherson, Moody, Roberts.
26. *Hesperia nevada* (Scudder)—Pennington.
27. *Polites peckius* (W. Kirby)—Aurora, Brookings, Brown, Codington, Corson, Custer, Davison, Day, Deuel, Douglas, Hamlin, Hanson, Harding, Lawrence, Lincoln, Marshall, McPherson, Minnehaha, Moody, Pennington, Roberts, Tripp, Union, Yankton.
28. *Polites themistocles* (Latreille)—Aurora, Brookings, Brown, Brule, Clay, Codington, Custer, Davison, Day, Deuel, Fall River, Gregory, Hamlin, Hand, Hanson, Harding,



- Hughes, Hyde, Jones, Lawrence, Lyman, Marshall, McPherson, Meade, Mellette, Minnehaha, Moody, Pennington, Roberts, Stanley, Tripp, Turner, Union, Yankton.
29. *Polites origenes rhena* (W. H. Edwards)—Brookings, Codington, Custer, Day, Fall River, Harding, Lawrence, Marshall, Meade, Pennington, Shannon, Union.
  30. *Polites mystic dacotah* (W. H. Edwards)—Aurora, Bennett, Brookings, Brown, Clark, Codington, Custer, Day, Deuel, Douglas, Fall River, Hamlin, Kingsbury, Lake, Lawrence, Lincoln, Marshall, McPherson, Meade, Mellette, Minnehaha, Moody, Pennington, Roberts, Spink, Todd.
  31. *Wallengrenia egeremet* (Scudder)—Brookings, Day, Deuel, Marshall, Roberts.
  32. *Pompeius verna* (W. H. Edwards)—Hutchinson, Turner, Yankton.
  33. *Atalopedes campestris campestris* (Boisduval)—Bon Homme, Brookings, Brown, Charles Mix, Clay, Codington, Custer, Day, Deuel, Fall River, Grant, Gregory, Hughes, Jackson, Lake, Lawrence, Lincoln, Marshall, McPherson, Meade, Minnehaha, Roberts, Shannon, Spink, Stanley, Todd, Tripp, Union, Yankton.
  34. *Atrytone arogos iowa* (Scudder)—Brookings, Brown, Custer, Day, Deuel, Fall River, Gregory, Lawrence, McPherson, Meade, Roberts, Stanley, Todd, Tripp.
  35. *Atrytone logan lagus* (W. H. Edwards)—Brookings, Brule, Clay, Codington, Corson, Custer, Day, Deuel, Douglas, Edmunds, Fall River, Grant, Gregory, Hamlin, Hand, Harding, Hughes, Hutchinson, Jerauld, Kingsbury, Marshall, McCook, McPherson, Meade, Mellette, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Spink, Tripp, Union, Walworth, Yankton, Ziebach.
  36. *Ochlodes sylvanoides napa* (W. H. Edwards)—Butte, Lawrence, Meade.
  37. *Poanes massasoit massasoit* (Scudder)—Brookings, Roberts.
  38. *Poanes hobomok hobomok* (Harris)—Brookings, Brule, Charles Mix, Custer, Davison, Day, Deuel, Douglas, Fall River, Haakon, Harding, Hughes, Jerauld, Lake, Lawrence, Lyman, Marshall, McCook, Mellette, Minnehaha, Pennington, Roberts, Stanley, Tripp, Turner, Union.
  39. *Poanes zabulon* (Boisduval and Le Conte)—Brule.
  40. *Poanes taxiles* (W. H. Edwards)—Custer, Fall River, Lawrence, Meade, Pennington.
  41. *Poanes viator viator* (W. H. Edwards)—Brookings, Day, Deuel, Roberts.
  42. *Euphyes vestris kiowah* (Reakirt)—Brookings, Brule, Custer, Day, Fall River, Harding, Lawrence, Marshall, Minnehaha, Pennington, Perkins, Roberts, Stanley, Sully, Todd, Tripp, Walworth.
  - 43a. *Atrytonopsis hianna* sp.—Day, Marshall, McPherson, Roberts.
  - 43b. *Atrytonopsis hianna turneri* H. A. Freeman—Bennett, Fall River, Haakon, Harding, Jones, Lyman, Meade, Mellette, Pennington, Perkins, Shannon.
  44. *Amblyscirtes simius* W. H. Edwards—Custer, Fall River, Meade, Pennington.
  45. *Amblyscirtes osleri* (Skinner)—Custer, Fall River, Haakon, Harding, Lawrence, Meade, Mellette, Pennington.
  46. *Amblyscirtes vialis* (W. H. Edwards)—Brookings, Charles Mix, Custer, Day, Fall River, Gregory, Haakon, Harding, Hughes, Hutchinson, Jackson, Jones, Lawrence, Lincoln, Meade, Mellette, Pennington, Perkins, Sanborn, Shannon, Sully, Todd, Tripp, Walworth.
  47. *Lerodea eufala* (W. H. Edwards)—Day, Minnehaha.
  48. *Megathymus streckeri leussleri* Holland—Custer, Fall River, Harding, Jackson, Lawrence, Meade, Pennington, Stanley, Todd, Ziebach.

## Superfamily Papilionoidea

### Family Papilionidae

49. *Parnassius phoebus sayti* W. H. Edwards—Custer, Lawrence, Meade, Pennington.
50. *Battus philenor philenor* (Linnaeus)—Brookings, Minnehaha.
51. *Eurytides marcellus* (Cramer)—Minnehaha.
52. *Papilio polyxenes asterius* Stoll—Bennett, Bon Homme, Brookings, Brown, Brule, Charles Mix, Custer, Davison, Day, Deuel, Fall River, Grant, Haakon, Hand, Hughes, Lawrence, Marshall, Minnehaha, Potter, Roberts, Stanley, Turner, Union, Yankton.

53. *Papilio bairdii bairdii* W. H. Edwards—Custer, Fall River, Harding, Pennington, Shannon, Stanley.
54. *Papilio zelicaon nitra* W. H. Edwards—Butte, Custer, Fall River, Harding, Lawrence, McPherson, Meade, Pennington, Perkins, Shannon, Ziebach.
55. *Papilio indra indra* Reakirt—Custer, Fall River, Lawrence, Pennington.
56. *Heracles cresphontes* (Cramer)—Brookings, Codington, Lincoln, Minnehaha, Union, Yankton.
57. *Pterourus glaucus glaucus* (Linnaeus)—Brookings, Brown, Brule, Charles Mix, Codington, Davison, Day, Deuel, Douglas, Faulk, Gregory, Hamlin, Hand, Hughes, Hutchinson, Hyde, Jerauld, Kingsbury, Lake, Lincoln, Lyman, Marshall, McCook, Mellette, Miner, Minnehaha, Moody, Roberts, Spink, Stanley, Tripp, Turner, Union, Walworth, Yankton.
58. *Pterourus canadensis* (Rothschild and Jordan)—Custer, Fall River, Lawrence, Meade, Pennington, Roberts.
59. *Pterourus rutulus rutulus* (Lucas)—Custer, Fall River, Lawrence, Pennington.
60. *Pterourus multicaudatus* (W. F. Kirby)—Brule, Custer, Fall River, Harding, Lawrence, Meade, Pennington, Shannon, Todd.
61. *Pterourus eurymedon* (Lucas)—Lawrence, Pennington.
62. *Pterourus troilus troilus* (Linnaeus)—Minnehaha, Pennington.

### Family Pieridae

63. *Neophasia menapia menapia* (C. and R. Felder)—Custer, Fall River, Lawrence, Meade, Pennington.
64. *Pontia sisymbrii nordini* (K. Johnson)—Custer, Fall River, Harding, Lawrence, Pennington.
65. *Pontia protodice* (Boisduval and Le Conte)—Beadle, Bennett, Brookings, Brule, Buffalo, Butte, Charles Mix, Clay, Corson, Custer, Davison, Day, Douglas, Fall River, Gregory, Hand, Harding, Hughes, Hutchinson, Hyde, Jackson, Jones, Lawrence, Lincoln, Lyman, McCook, McPherson, Meade, Miner, Minnehaha, Pennington, Potter, Sanborn, Shannon, Spink, Stanley, Sully, Tripp, Turner, Union, Yankton.
66. *Pontia occidentalis occidentalis* (Reakirt)—Bennett, Brule, Butte, Corson, Custer, Day, Fall River, Hughes, Hyde, Lawrence, Lyman, McPherson, Mellette, Pennington, Sanborn, Stanley, Sully, Walworth, Ziebach.
- 67a. *Pieris napi oleracea* Harris—Marshall, Roberts.
- 67b. *Pieris napi mcdunnoughi* Remington—Lawrence.
68. *Pieris rapae* (Linnaeus)—Aurora, Bennett, Bon Homme, Brookings, Brown, Brule, Buffalo, Campbell, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Douglas, Edmunds, Fall River, Faulk, Grant, Gregory, Haakon, Hamlin, Hand, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Moody, Pennington, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton.
69. *Ascia monuste* ssp.—Brown.
70. *Euchloe ausonides palaeoreios* K. Johnson—Custer, Lawrence, Meade, Pennington.
71. *Euchloe olympia* W. H. Edwards—Bennett, Brookings, Brule, Butte, Campbell, Clay, Corson, Custer, Dewey, Fall River, Haakon, Harding, Hughes, Jackson, Jones, Lawrence, Lyman, Marshall, McPherson, Meade, Mellette, Minnehaha, Pennington, Perkins, Potter, Shannon, Stanley, Sully, Todd, Union, Yankton, Ziebach.
72. *Anthocharis sara julia* W. H. Edwards—Lawrence.
73. *Colias philodice* ssp.—Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clark, Clay, Codington, Corson, Custer, Day, Deuel, Dewey, Douglas, Edmunds, Fall River, Faulk, Grant, Haakon, Hamlin, Hand, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.

74. *Colias eurytheme* Boisduval—Aurora, Beadle, Bennett, Bon Homme, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Douglas, Edmunds, Fall River, Faulk, Grant, Gregory, Haakon, Hamlin, Hand, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
- 75a. *Colias alexandra alexandra* W. H. Edwards—Custer, Fall River, Jackson, Pennington.
- 75b. *Colias alexandra krauthii* Klotz—Custer, Fall River, Lawrence, Pennington.
76. *Zerene cesonia cesonia* (Stoll)—Brookings, Butte, Charles Mix, Corson, Fall River, Gregory, Hughes, Minnehaha, Pennington, Roberts, Sanborn, Stanley, Union, Yankton.
77. *Phoebis sennae eubule* (Linnaeus)—Clay, Minnehaha, Union.
78. *Phoebis agarithe agarithe* (Boisduval)—Brookings, Minnehaha.
79. *Eurema daira daira* (Godart)—Minnehaha.
80. *Eurema mexicanum* (Boisduval)—Corson, Custer, Minnehaha, Pennington.
81. *Eurema lisa lisa* (Boisduval and Le Conte)—Brookings, Clay, Day, Hughes, Minnehaha, Union, Yankton.
82. *Eurema nicippe* (Cramer)—Minnehaha.
83. *Nathalis iole* Boisduval—Bon Homme, Brookings, Charles Mix, Clay, Custer, Day, Deuel, Fall River, Gregory, Hughes, Jackson, Lawrence, Lyman, Minnehaha, Roberts, Sanborn, Stanley, Turner, Union, Yankton.

### Family Lycaeidae

84. *Feniseca tarquinius tarquinius* (Fabricius)—Roberts.
85. *Lycaena phlaeas americana* Harris—Brown, Jackson, Meade.
86. *Gaeides xanthoides dione* (Scudder)—Bennett, Brookings, Brule, Buffalo, Charles Mix, Clay, Corson, Custer, Day, Deuel, Douglas, Fall River, Grant, Gregory, Harding, Hughes, Jackson, Jones, Lawrence, Lyman, Marshall, McPherson, Meade, Minnehaha, Pennington, Perkins, Potter, Shannon, Stanley, Sully, Todd, Tripp.
87. *Hylolycaena hyllus* (Cramer)—Beadle, Bennett, Brookings, Brule, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Edmunds, Fall River, Faulk, Grant, Gregory, Hamlin, Hand, Hanson, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lawrence, Lyman, Marshall, McPherson, Meade, Mellette, Miner, Minnehaha, Moody, Pennington, Potter, Roberts, Shannon, Spink, Sully, Todd, Tripp, Turner, Union, Yankton.
88. *Chalceria rubida longi* (K. Johnson and Balogh)—Butte, Custer, Harding, Lawrence, Meade, Pennington.
89. *Epidemia helloides* (Boisduval)—Bennett, Brookings, Brule, Butte, Clark, Custer, Day, Dewey, Haakon, Harding, Hughes, Jackson, Jones, Lawrence, Marshall, Meade, Mellette, Minnehaha, Pennington, Potter, Roberts, Shannon, Stanley, Todd, Tripp.
90. *Harknclenus titus titus* (Fabricius)—Bennett, Bon Homme, Brookings, Brule, Charles Mix, Codington, Day, Deuel, Fall River, Grant, Gregory, Harding, Hughes, Lawrence, Marshall, Meade, Pennington, Potter, Roberts, Stanley, Sully, Todd, Tripp, Union, Walworth, Ziebach.
91. *Satyrium acadicum montanensis* (Watson and W. P. Comstock)—Beadle, Brookings, Brown, Kingsbury, Lawrence, Lyman, McCook, Meade, Pennington, Todd, Tripp.
92. *Satyrium edwardsii* (Grote and Robinson)—Roberts.
93. *Satyrium calanus falacer* (Godart)—Brule, Charles Mix, Day, Deuel, Lawrence, Meade, Minnehaha, Roberts, Sully, Tripp, Union.
94. *Satyrium caryaevorum* (McDunnough)—Lawrence.
95. *Satyrium liparops* ssp.—Day, Harding, Hughes, Jackson, Lawrence, Lyman, Minnehaha, Pennington.

96. *Mitoura siva siva* (W. H. Edwards)—Brule, Custer, Fall River, Haakon, Harding, Hughes, Jackson, Jones, Lyman, Meade, Mellette, Pennington, Shannon, Ziebach.
97. *Mitoura grynea grynea* (Hübner)—Union.
98. *Incisalia augustinus iroides* (Boisduval)—Custer, Lawrence, Meade, Pennington.
99. *Incisalia polia obscura* Ferris and Fisher—Custer, Lawrence, Pennington.
100. *Incisalia eryphon eryphon* (Boisduval)—Custer, Fall River, Harding, Lawrence, Meade, Pennington, Todd.
101. *Strymon melinus atrofasciatus* McDunnough—Bennett, Bon Homme, Brookings, Brule, Butte, Charles Mix, Clay, Custer, Davison, Day, Fall River, Gregory, Haakon, Harding, Hughes, Jackson, Lawrence, Lyman, McCook, Meade, Mellette, Minnehaha, Pennington, Shannon, Stanley, Sully, Todd, Tripp, Union, Yankton, Ziebach.
102. *Leptotes marina* (Reakirt)—Minnehaha, Pennington.
103. *Hemiargus isola alce* (W. H. Edwards)—Brookings, Butte, Clay, Codington, Custer, Day, Fall River, Haakon, Hamlin, Hanson, Harding, Hughes, Jones, Lawrence, Lyman, Marshall, Meade, Minnehaha, Pennington, Stanley, Sully, Todd, Tripp, Union, Yankton, Ziebach.
104. *Everes comyntas atomyntas* (Godart)—Brookings, Brown, Campbell, Charles Mix, Clay, Codington, Custer, Davison, Day, Faulk, Grant, Gregory, Haakon, Hamlin, Harding, Hughes, Jackson, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Mellette, Minnehaha, Moody, Pennington, Potter, Roberts, Sully, Todd, Tripp, Union, Walworth, Yankton.
105. *Everes amyntula valeriae* Clench—Custer, Fall River, Harding, Lawrence, Pennington.
106. *Celastrina argiolus* ssp.—Beadle, Brookings, Brule, Clay, Codington, Custer, Davison, Day, Deuel, Dewey, Douglas, Fall River, Hanson, Harding, Hughes, Jerauld, Kingsbury, Lake, Lawrence, Lincoln, Marshall, McPherson, Meade, Minnehaha, Moody, Pennington, Roberts, Shannon, Stanley, Union, Yankton.
107. *Glaucopsyche piasus daunia* (W.H. Edwards)—Custer, Harding, Lawrence, Pennington.
108. *Glaucopsyche lygdamus oro* (Scudder)—Butte, Campbell, Corson, Custer, Day, Dewey, Fall River, Harding, Hughes, Jackson, Jones, Lawrence, Marshall, Meade, Mellette, Pennington, Perkins, Shannon, Stanley, Sully.
109. *Lycaeides melissa melissa* (W. H. Edwards)—Aurora, Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Douglas, Edmunds, Fall River, Faulk, Grant, Gregory, Haakon, Hamlin, Hanson, Harding, Hughes, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Union, Walworth, Yankton, Ziebach.
110. *Plebejus saepiolus saepiolus* (Boisduval)—Custer, Fall River, Harding, Lawrence, Meade, Pennington.
111. *Icaricia icarioides lycea* (W. H. Edwards)—Custer, Harding, Lawrence, Pennington.
112. *Icaricia shasta minnehaha* (Scudder)—Lawrence, Pennington.
113. *Icaricia acmon lutzi* (dos Passos)—Bennett, Butte, Custer, Day, Fall River, Harding, Jackson, Lawrence, Meade, Mellette, Pennington, Perkins, Todd.
114. *Agriades rusticus rusticus* (W. H. Edwards)—Custer, Lawrence, Pennington.

### Family Riodinidae

115. *Apodemia mormo mormo* (C. and R. Felder)—Pennington.

### Family Libytheidae

116. *Libytheana bachmanii bachmanii* (Kirkland)—Brookings, Clay, Davison, Day, Minnehaha, Yankton.

## Family Heliconiidae

117. *Agraulis vanillae incarnata* (Riley)—Butte, Minnehaha, Pennington.

## Family Nymphalidae

118. *Euptoieta claudia* (Cramer)—Bennett, Bon Homme, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clay, Codington, Custer, Davison, Day, Deuel, Dewey, Douglas, Fall River, Faulk, Grant, Hamlin, Hand, Harding, Hughes, Jackson, Jones, Kingsbury, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
119. *Speyeria cybele cybele* (Fabricius)—Brookings, Brule, Clay, Corson, Custer, Day, Deuel, Dewey, Faulk, Grant, Gregory, Hamlin, Harding, Hutchinson, Hyde, Jackson, Jones, Lawrence, Lincoln, Lyman, Marshall, McCook, Meade, Miner, Minnehaha, Pennington, Perkins, Potter, Roberts, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton.
120. *Speyeria aphrodite alcestris* (W. H. Edwards)—Brookings, Codington, Corson, Custer, Day, Deuel, Fall River, Grant, Haakon, Harding, Hughes, Lawrence, Marshall, McPherson, Meade, Minnehaha, Pennington, Perkins, Roberts, Shannon, Union, Walworth, Ziebach.
121. *Speyeria idalia* (Drury)—Beadle, Bennett, Bon Homme, Brookings, Brown, Brule, Campbell, Charles Mix, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Douglas, Fall River, Faulk, Grant, Gregory, Haakon, Hamlin, Hanson, Hughes, Hutchinson, Hyde, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Minnehaha, Moody, Pennington, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
122. *Speyeria edwardsii* (Reakirt)—Bennett, Brule, Butte, Custer, Dewey, Fall River, Harding, Hughes, Jackson, Jones, Lawrence, Lyman, McPherson, Meade, Mellette, Pennington, Shannon, Stanley, Sully, Todd.
123. *Speyeria coronis* ssp.—Custer, Fall River, Harding, Lawrence, Pennington.
124. *Speyeria zerene garretti* (Gunder)—Custer, Harding, Lawrence, Pennington.
125. *Speyeria callippe calgariana* (McDunnough)—Campbell, Custer, Fall River, Harding, Lawrence, McPherson, Meade, Pennington, Perkins, Ziebach.
- 126a. *Speyeria atlantis* ssp.—Custer, Lawrence, Pennington.
- 126b. *Speyeria atlantis lurana* dos Passos and Grey—Custer, Lawrence, Meade, Pennington.
127. *Speyeria mormonia eurynome* (W. H. Edwards)—Custer, Lawrence, Pennington, Shannon.
- 128a. *Clossiana selene myrina* (Cramer)—Brookings, Brown, Codington, Day, Deuel, Grant, Marshall, McPherson, Roberts.
- 128b. *Clossiana selene nebraskensis* (Holland)—Bennett, Mellette, Todd.
- 128c. *Clossiana selene sabulocollis* (Kohler)—Custer, Lawrence, Pennington.
129. *Clossiana bellona toddi* (Holland)—Brookings, Brown, Clay, Day, Deuel, Grant, Kingsbury, Marshall, Miner, Minnehaha, Moody, Roberts.
130. *Charidryas gorgone carlota* (Reakirt)—Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Butte, Charles Mix, Corson, Custer, Day, Dewey, Fall River, Faulk, Haakon, Harding, Hughes, Hutchinson, Hyde, Jones, Lawrence, Lyman, Marshall, McPherson, Meade, Mellette, Minnehaha, Pennington, Perkins, Shannon, Spink, Stanley, Todd, Tripp, Union, Yankton, Ziebach.
131. *Charidryas nycteis nycteis* (Doubleday and Hewitson)—Bennett, Brookings, Brule, Clay, Custer, Day, Deuel, Dewey, Gregory, Hyde, Lawrence, Marshall, Minnehaha, Pennington, Roberts, Todd, Yankton.
132. *Charidryas acastus* (W. H. Edwards)—Brule, Custer, Harding, Hughes, Stanley.
133. *Anthanassa texana texana* (W. H. Edwards)—Roberts.
134. *Phyciodes tharos tharos* (Drury)—Beadle, Bennett, Brookings, Brown, Brule, Buf-

- falo, Butte, Campbell, Charles Mix, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Douglas, Fall River, Faulk, Grant, Gregory, Haakon, Harding, Hughes, Hutchinson, Hyde, Jackson, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
135. *Phyciodes pascoensis* W. G. Wright—Brookings, Custer, Day, Deuel, Grant, Harding, Jackson, Lawrence, Marshall, Pennington, Roberts.
  136. *Phyciodes batesii* (Reakirt)—Custer, Lawrence, Meade, Pennington.
  137. *Phyciodes pratensis camillus* W. H. Edwards—Fall River, Lawrence.
  138. *Phyciodes pallidus barnesi* Skinner—Custer, Fall River, Lawrence.
  139. *Euphydryas anicia bernadetta* Leussler—Butte, Custer, Fall River, Harding, Lawrence, Pennington.
  140. *Polygonia interrogationis* (Fabricius)—Bon Homme, Brookings, Brule, Charles Mix, Clay, Davison, Day, Deuel, Faulk, Grant, Hughes, Hyde, Lake, Lincoln, Marshall, Meade, Mellette, Minnehaha, Pennington, Roberts, Stanley, Todd, Turner, Union, Walworth, Yankton.
  141. *Polygonia comma* (Harris)—Brookings, Charles Mix, Clay, Custer, Day, Deuel, Dewey, Gregory, Hand, Hughes, Hutchinson, Hyde, Lincoln, Lyman, Marshall, Minnehaha, Potter, Roberts, Turner, Walworth, Yankton.
  142. *Polygonia satyrus* (W. H. Edwards)—Custer, Lawrence, Pennington.
  143. *Polygonia faunus* ssp.—Custer, Fall River, Lawrence, Meade, Pennington.
  144. *Polygonia zephyrus* (W. H. Edwards)—Custer, Fall River, Lawrence, Meade, Pennington.
  145. *Polygonia progne progne* (Cramer)—Brookings, Brule, Custer, Day, Fall River, Harding, Lawrence, Lincoln, Minnehaha, Pennington, Roberts, Yankton.
  146. *Nymphalis vau-album j-album* (Boisduval and Le Conte)—Brookings, Custer, Lawrence, Marshall, Meade, Pennington, Roberts.
  147. *Nymphalis californica californica* (Boisduval)—Brookings, Lawrence.
  148. *Nymphalis antiopa antiopa* (Linnaeus)—Bennett, Brookings, Brown, Brule, Butte, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Fall River, Faulk, Grant, Hand, Harding, Hughes, Hutchinson, Jackson, Jerauld, Jones, Lake, Lawrence, Lincoln, Lyman, Marshall, McPherson, Meade, Mellette, Miner, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Shannon, Stanley, Sully, Todd, Tripp, Turner, Union, Yankton, Ziebach.
  149. *Aglais milberti milberti* (Godart)—Brookings, Custer, Day, Deuel, Fall River, Harding, Hughes, Lawrence, Meade, Minnehaha, Pennington, Perkins, Shannon, Stanley.
  150. *Vanessa virginiensis* (Drury)—Brookings, Butte, Codington, Custer, Day, Deuel, Edmunds, Fall River, Jackson, Lawrence, Meade, Minnehaha, Pennington, Stanley, Turner, Union, Yankton.
  151. *Vanessa cardui* (Linnaeus)—Aurora, Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Edmunds, Fall River, Faulk, Grant, Gregory, Haakon, Hamlin, Hand, Hanson, Harding, Hughes, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Miner, Minnehaha, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
  152. *Vanessa annabella* (Field)—Pennington.
  153. *Vanessa atalanta rubria* (Fruhstorfer)—Beadle, Bennett, Brookings, Brown, Brule, Butte, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Douglas, Edmunds, Fall River, Faulk, Grant, Gregory, Haakon, Hamlin, Hand, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McPherson, Meade, Mellette, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
  154. *Junonia coenia* Hübner—Aurora, Brookings, Brown, Brule, Charles Mix, Clay, Cod-

- ington, Custer, Day, Deuel, Edmunds, Lincoln, Minnehaha, Tripp, Turner, Union, Yankton.
- 155a. *Basilarchia arthemis arthemis* (Drury)—Brookings, Day, Marshall, Roberts.
- 155b. *Basilarchia arthemis rubrofasciata* Barnes and McDunnough—Brookings, Brown, Day, Deuel, Marshall, Minnehaha, Roberts.
- 155c. *Basilarchia arthemis astyanax* (Fabricius)—Brookings, Charles Mix, Clark, Clay, Codington, Davison, Day, Deuel, Grant, Hamlin, Hand, Hughes, Kingsbury, Lincoln, Marshall, Minnehaha, Moody, Roberts, Stanley, Turner, Union, Yankton.
156. *Basilarchia archippus archippus* (Cramer)—Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Charles Mix, Clark, Clay, Davison, Day, Deuel, Douglas, Fall River, Grant, Hand, Hanson, Hughes, Hutchinson, Hyde, Jackson, Jones, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, Miner, Minnehaha, Moody, Pennington, Potter, Roberts, Sanborn, Shannon, Stanley, Sully, Todd, Turner, Union, Yankton.
157. *Basilarchia weidemeyerii oberfoelli* (F. M. Brown)—Custer, Fall River, Harding, Jackson, Lawrence, Meade, Pennington, Perkins, Shannon, Todd.
158. *Mestra amymone* (Ménétriés)—Brookings.
159. *Anaea andria* Scudder—Shannon, Todd, Tripp.
160. *Asterocampa celtis celtis* (Boisduval and Le Conte)—Brookings, Brule, Buffalo, Charles Mix, Clay, Davison, Day, Fall River, Grant, Hughes, Hutchinson, Kingsbury, Lincoln, Marshall, McCook, Minnehaha, Roberts, Stanley, Todd, Tripp, Turner, Union, Walworth, Yankton.
161. *Asterocampa clyton clyton* (Boisduval and Le Conte)—Brookings, Day, Kingsbury, Lincoln, Minnehaha, Yankton.

### Family Satyridae

162. *Enodia anthedon* A. H. Clark—Day, Deuel, Lincoln, Marshall, Minnehaha, Roberts, Tripp.
163. *Satyroides eurydice* ssp.—Bennett, Brookings, Corson, Day, Deuel, Grant, Hamlin, Hughes, Marshall, McCook, Moody, Roberts, Todd, Tripp.
164. *Megisto cymela cymela* (Cramer)—Aurora, Bennett, Bon Homme, Brookings, Brule, Charles Mix, Clark, Clay, Corson, Day, Deuel, Douglas, Faulk, Gregory, Harding, Hughes, Hutchinson, Jerauld, Lawrence, Lincoln, Marshall, Minnehaha, Roberts, Sanborn, Stanley, Sully, Tripp, Turner, Union, Yankton.
- 165a. *Coenonympha tullia* ssp.—Aurora, Bennett, Brookings, Brule, Charles Mix, Codington, Corson, Davison, Day, Deuel, Dewey, Grant, Gregory, Haakon, Hamlin, Hughes, Jackson, Jerauld, Jones, Lake, Lyman, Marshall, McPherson, Mellette, Minnehaha, Perkins, Potter, Roberts, Sanborn, Shannon, Stanley, Sully, Todd, Tripp, Turner, Walworth, Ziebach.
- 165b. *Coenonympha tullia benjamini* McDunnough—Butte, Custer, Fall River, Harding, Lawrence, Meade, Pennington.
166. *Cercyonis pegala* spp.—Aurora, Bennett, Bon Homme, Brookings, Brown, Brule, Buffalo, Butte, Campbell, Charles Mix, Clark, Clay, Codington, Corson, Custer, Davison, Day, Deuel, Dewey, Douglas, Edmunds, Fall River, Faulk, Grant, Gregory, Hamlin, Hand, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Meade, Mellette, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Shannon, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton, Ziebach.
167. *Cercyonis meadii meadii* (W. H. Edwards)—Fall River, Harding, Lawrence, Meade, Pennington.
168. *Cercyonis oetus charon* (W. H. Edwards)—Custer, Harding, Lawrence, Meade, Pennington, Perkins.
169. *Neominois ridingsii ridingsii* (W. H. Edwards)—Pennington.
170. *Oeneis chryxus chryxus* (Doubleday and Hewitson)—Pennington.
171. *Oeneis uhleri* ssp.—Brookings, Brown, Butte, Custer, Day, Fall River, Harding, Lawrence, Marshall, McPherson, Pennington, Perkins, Potter, Roberts, Shannon.

## Family Danaidae

172. *Danaus plexippus* (Linnaeus)—Aurora, Beadle, Bennett, Brookings, Brown, Brule, Buffalo, Campbell, Charles Mix, Clark, Clay, Codington, Custer, Davison, Day, Deuel, Douglas, Fall River, Faulk, Grant, Gregory, Hamlin, Hand, Hanson, Harding, Hughes, Hutchinson, Hyde, Jackson, Jerauld, Jones, Kingsbury, Lake, Lawrence, Lincoln, Lyman, Marshall, McCook, McPherson, Miner, Minnehaha, Moody, Pennington, Perkins, Potter, Roberts, Sanborn, Spink, Stanley, Sully, Todd, Tripp, Turner, Union, Walworth, Yankton.

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## BIOLOGY OF *ANAEA RYPHEA* (NYMPHALIDAE) IN CAMPINAS, BRAZIL

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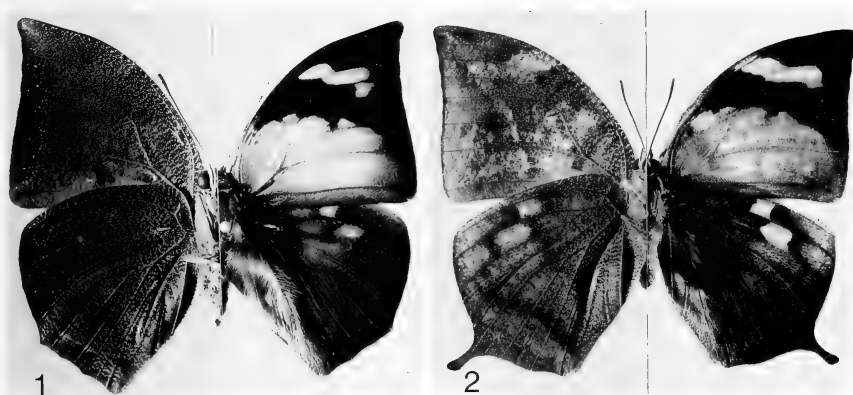
**ABSTRACT.** *Anaea ryphea* uses *Croton floribundus* (Euphorbiaceae) as its main larval food plant at Campinas, Brazil. Weekly censuses of the immature stages of *A. ryphea* were conducted from September 1988 to August 1989. Adults and larvae were found only from December through May. Females usually laid one egg per leaf and exhibited no plant height preference. Within individuals plants, most eggs were laid on the intermediate leaves; they were rare on the lowest and absent on the apical, new leaves. The complete life cycle in the field lasts 50 to 60 days. The pattern of development in *A. ryphea* is similar to that described for 5 other species of *Anaea*. The early stages resemble closely those described for *A. euryppyle*, which also uses a species of *Croton* as its larval food plant in El Salvador.

**Additional key words:** *Hypna clytemnestra*, life cycle, *Memphis*, *Croton*, Euphorbiaceae.

The genus *Anaea* Hübner includes most of the Neotropical Charaxinae, although use of the generic name varies considerably among authors. Comstock (1961) assigned to *Anaea* the species now considered members of the *Anaea troglodyta* group. He used *Memphis* Hübner, formerly described as a generic name, as a subgenus for most of the other species of *Anaea*, including the blue species and *A. ryphea* (Cramer). Rydon (1971) subdivided the group further, describing *Fountainea*, into which he transferred *ryphea*. Although the most recent treatment of the group (Descimon 1986) recognizes *Anaea* as distinct from *Fountainea*, other authors (e.g., DeVries 1987) include *Fountainea* species in *Memphis*. According to Hemming (1967), *Anaea* has priority, leaving *Memphis* a synonym.

During the last ten years, *Anaea andria* Scudder has been the subject of several studies, and its biology is now well known. It uses *Croton capitatus* (Euphorbiaceae) as its primary larval food plant in North America (Riley 1981, 1988, 1989). The life cycles of other species of *Anaea* have been reported by Muyschondt (1973, 1974a, 1974b, 1975a, 1975b); however, the early stages of *A. ryphea* have remained unknown. DeVries (1987) reported *Anaea ryphea* from Mexico to the Amazon Basin, but it has become evident that its distribution is wider than previously thought. In southern Brazil it uses *Croton floribundus* Spreng (Euphorbiaceae) as its primary larval food plant (Caldas 1991).

*Anaea ryphea* is sexually dimorphic: males are smaller and usually lack the tail-like expansion of the hindwing (Figs. 1 & 2). Males are bright orange, red, and purple, with blue distal bars on the forewing cells.



FIGS. 1-2. Ventral (left) and dorsal (right) views of adult *Anaea ryphea*. 1, male. 2, female.

Females always have the hindwing expansion ("tail"), dark brown bars on the forewing cells, and yellow and orange as the dominant colors on both wings. The species is found in tropical and subtropical forests, where it can be seen in rapid flight or perched on urine, feces, and rotten fruits. Herein I describe the life cycle of *A. ryphea* from south-eastern Brazil.

#### STUDY SITE AND METHODS

This study was conducted in the Santa Genebra Reserve, Campinas, São Paulo, Brazil (22°54'S, 47°05'W, elevation 650 m). The reserve includes 2,517,759 m<sup>2</sup> of disturbed subtropical semi-deciduous forest. Mean monthly temperature varies from 18°C to 29°C, with daily fluctuations of as much as 20°C from July to September. The dry season lasts from May through September. The rainy season may start with light rainfall or with heavy "summer storms." Frosts are rare, but may occur from July to September. Although the study was conducted from September 1988 through April 1991, the data presented here refer only to the first wet season, from December 1988 to May 1989.

I visited the reserve once a week from September 1988 through January 1989, then twice a week until mid-February. From then on, visits were more frequent, increasing to every other day until late April 1989, when they became weekly again.

*Croton floribundus* is a lactescent plant that can be either a small shrub or a tall tree, depending on its age and environmental conditions. The smallest plant found was only 20 cm tall, while the largest was more than 4 m. The leaves are alternate, stipulate, and grayish green.

Leaf size depends on plant height: 10 cm long on plants up to 2 m tall and 20 cm long on taller plants. The inflorescences are monoecious, with male flowers terminal. At the study site, flowers were seen during December. Other species of *Croton* are recorded as food plants for species of Nymphalidae (DeVries 1987) and Riodinidae (DeVries 1988). *Croton floribundus* is common in the Santa Genebra Reserve, in both sunny and shaded areas, as solitary individuals or in patches. It grows mostly along the edges of trails and is rare in the middle of the forest. The soil along the trails is mostly clay, and during the dry season the plants seem to resist desiccation. From May on, plants begin to dry out, sometimes being reduced to no more than a woody stem that puts out new leaves the next wet season. During the rainy season, the soil maintains a high water content. Along the reserve's central road (1,160 m long), I found 186 plants. All were mapped and marked for use in this study.

During each visit I checked all leaves for larvae on the 186 marked plants. Eggs were difficult to detect, so exact numbers were not known until the following season. Twenty eggs were collected and taken into the laboratory. These eggs were the source of hatching time observations. In the field, each leaf with a larva was individually numbered because larvae stay on the same leaf most of the time. All larvae were measured and identified as to instar. Their height from the ground and the general aspect of the leaf were noted. With this methodology I was able to (1) follow the growth of every individual, (2) determine the duration of each instar in the field, and (3) assess mortality for each instar.

## RESULTS AND DISCUSSION

### Oviposition

*Anaea ryphea* eggs are laid singly and usually one per leaf, in the central third of the under surface. Rarely, two or three eggs are laid. A similar oviposition pattern was described by Ramos (1984) for *Anaea troglodyta borinquenalis* and by Muyschondt (1975b) for *Anaea (Memphis) pithyusa*. Females fly around the plant, inspecting leaves quickly before ovipositing. I could not tell whether eggs laid on the same leaf came from the same female. Placing one egg per leaf could eliminate competition during the early instars, when larvae have restricted movement. In Colón Province, Republic of Panama, 1991, while studying the same species, I saw females placing more than one egg on the same leaf of *Croton billbergianus*, although not sequentially. In each of the three cases observed, the female flew from one leaf to another, ovi-

positing on acceptable leaves, eventually returning to oviposit on a leaf she already had used.

There was no plant height preference for oviposition among the 186 marked plants. All instars were found between 15 cm and 2 m above the ground, on short or tall plants. I did not include plants taller than 2 m in this study owing to the difficulty in reaching high leaves, but even on those, I could see active larvae when they were present. Within the same plant, though, larvae were found mostly on intermediate leaves, never on the apical ones, and rarely on the lower (older) ones. This distribution seems to be related to the age of the leaves, not to their height from the ground.

### Development and Behavior

After eclosion larvae eat the egg shell and move toward the apex of the leaf where they begin to feed on both sides of the midvein, which when exposed becomes their resting place. This behavior, common in Nymphalidae, also is considered common for other *Anaea* species (Muyshondt 1974a). Ramos (1984) reported that larvae of *A. troglodyta borinquenalis* build a perching place from the tip instead of exposing the midvein first. When not feeding, *A. ryphea* larvae remain on this vein facing the apex, grasping the vein with both thoracic and abdominal legs. It is rare to see a larva start feeding on another part of the leaf, but when this happens, a lateral vein is chosen and used in the same manner. In either case, an individual may add fecula ("frass chain") to the vein, perhaps to strengthen it. Fecula is added mostly when the vein is thin, whether it is a lateral or central one. It also may be used to extend the vein beyond its natural length.

From the third instar on, *A. ryphea* larvae may roll the leaf to form a tubular shelter, holding it closed with silk, although this behavior usually is observed from fourth instar on. They begin by laying silk over the entire area of leaf that is to be rolled. As they add to and strengthen the threads, the leaf begins to curve and roll itself into a tube. Normally, the apical portion of the leaf is used to construct the shelter. If the leaf is damaged by some external event such as bird attack or herbivores, the larva may move to another leaf. Change of leaf does not necessarily follow any special rule, and I have observed larvae moving to new and old leaves, above or below the original one. The tube is open at both ends, but the opening that faces the base of the leaf is the larger of the two and is used by the larvae as the entrance and exit. The smaller opening is used to dispose of fecula. In order to enter the tube, the larva approaches close to opening, then makes a u-turn and backs into the shelter.

I did not measure leaf consumption, but observations show that larvae

usually feed on the same leaf through the third instar, reducing it to one-half or one-third its original size. From third instar on, feeding increases noticeably. Larvae can move to another leaf and build a new tube if the first leaf is consumed before pupation, but that rarely was seen. More commonly they visit another leaf just to eat, then return to the old leaf where the shelter is kept (they never eat the roll). Feeding takes place mainly from dusk to dark, as do molting and pupation. When not eating, larvae remain on the midvein or inside the tube. During the last instar, the larva abandons the plant and searches for a suitable place to pupate.

### Early Stages

**Egg** (Fig. 3). Approximately 1 mm in diameter ( $n = 10$ ). Spherical, with small depression on top (micropyle end), greenish white, with no conspicuous sculpturing. Duration 5–6 days.

**First Instar** (Fig. 5). Length 1.5–8.0 mm ( $n = 1161$ ). Head brown with dark brown spots, lighter near foramen; epicranial suture complete, well marked. Body eruciform, hazel, darker posteriorly. Duration approximately 6 days ( $n = 278$ ).

**Second Instar** (Fig. 4). Length 5–14 mm ( $n = 598$ ). Head light brown with three dark stripes on each side; frons with central dark stripe; pair of small scoli (each with two setae) on vertex, scattered chalazae restricted to sides of head. Body pale greenish brown with pale spots throughout, slightly enlarged on second abdominal segment. Duration approximately 6 days ( $n = 155$ ).

**Third Instar** (Fig. 6). Length 8–20 mm ( $n = 308$ ). Head similar to that of second instar, but with a series of dark spots between the three dark stripes of the epicranium, also some dark dots around the foramen; scoli larger than on second instar, with more chalazae. Body green, except second, fifth, and seventh abdominal tergite, which are brown; second abdominal segment enlarged, forming a small dorsal hump. Duration approximately 7 days ( $n = 105$ ).

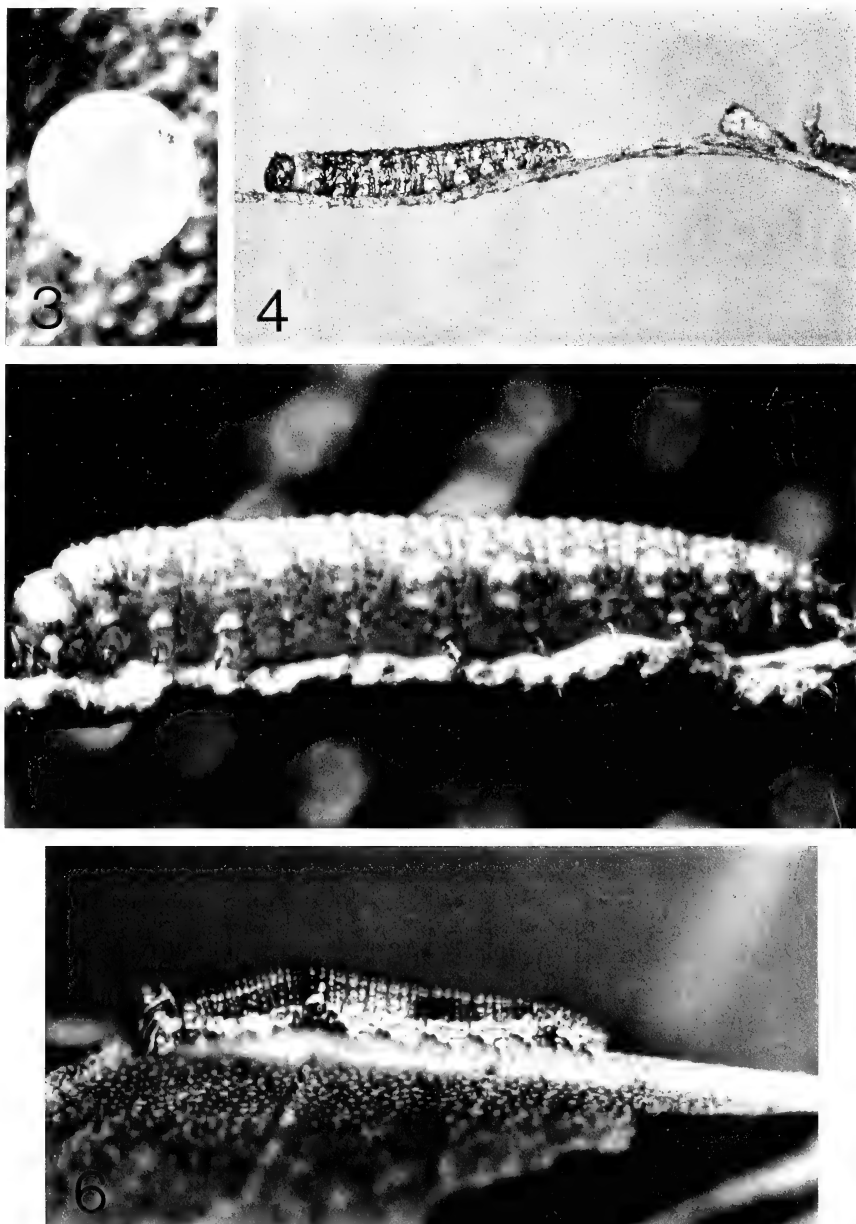
**Fourth Instar** (Fig. 7). Length 14–24 mm ( $n = 301$ ). Head similar to third instar, with dark stripes more pronounced, scoli resembling antlers, and chalazae all over head. Body brownish green, with dark brown subdorsal stripes following second and third thoracic segments, turning dorsal and joining to form a broad dorsal band across the first and second abdominal segments; fourth through tenth abdominal segments also with dark brown subdorsal stripe; third abdominal segment entirely green. Hump on second abdominal segment more conspicuous than in previous instar. Duration approximately 7 days ( $n = 83$ ).

**Fifth Instar** (Fig. 8). Length 20–28 mm ( $n = 273$ ). Remarkably distinct from previous instars. Head green; scoli large, Y-shaped; chalazae present in greater density. Body bright green, with black dots on dorsal and lateral surfaces of all segments; second, fifth, and seventh abdominal segments with reddish hazel subdorsal stripes. Duration 8–15 days ( $n = 45$ ).

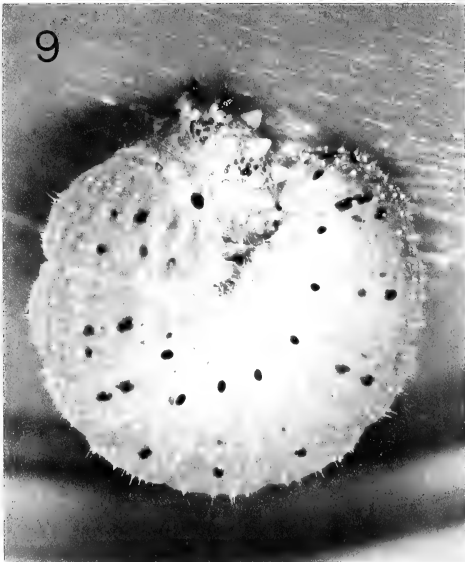
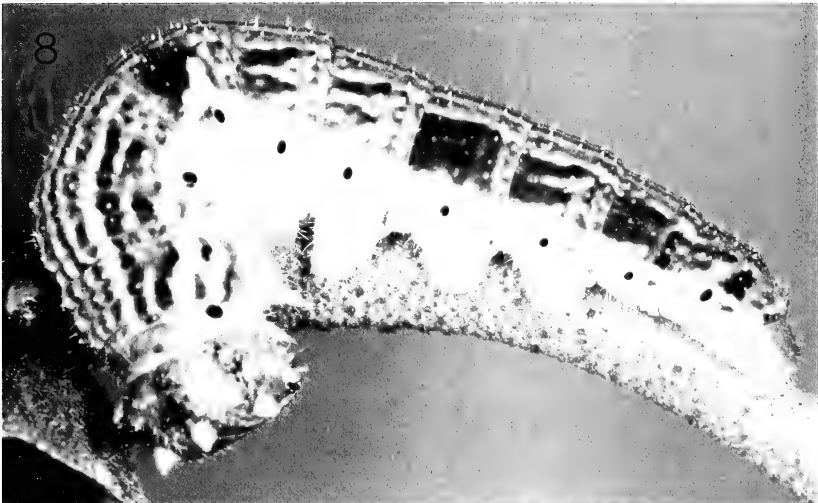
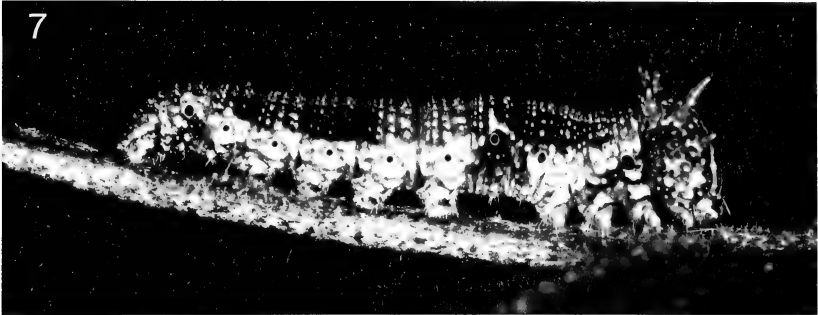
**Pre-pupa** (Fig. 9). Green, curled horizontally rather than vertically as in other nymphalids, and appressed to its support. Duration 2 days ( $n = 12$ ).

**Pupa** (Fig. 10). Green, naked; dark cremaster attached to white silken pad. Duration approximately 12 days ( $n = 12$ ).

The duration of the early stages in the field requires 50–60 days, accounting for individual variation. The pattern of development of *Anaea ryphea* is similar to that described for *Anaea (Zaretis) itys* on



FIGS. 3-6. Early stages of *Anaea ryphea*. 3, Egg on *Croton billbergianus* leaf. 4, Second instar larva with frass chain. 5, First instar. 6, Third instar larva.





*Casearia nitida* (L.) Jacq. (Flacouidaceae) (Muyschondt 1973); for *Anaea* (*Consul*) *fabi*us Doubleday on *Piper tuberculatum* Jacquin, *P. auritum* H.B.K., and *P. umbellatum* L. (Piperaceae) (Muyschondt 1974a); and for *Anaea* (*Memphis*) *pithyusa* on *Croton reflexifolius* H.B.K. and *C. niveus* Jacquin (Euphorbiaceae) (Muyschondt 1975b), all of which were reared in the laboratory from field collected eggs. The eggs of the four species (including *A. ryphea*) are similar, and instars show minor variations. Duration of development is slightly shorter in *A. (Zaretis) itys* and *A. (Memphis) pithyusa*, and longer in *A. (Consul) fabius*. It is likely that the differences observed in the laboratory also would be present under field conditions. *Anaea (Zaretis) itys* differs from the others in that it does not build a leaf roll. Instead, it remains at the tip of the leaf until the pre-pupal stage. In all four species, the pre-pupae curl horizontally instead of vertically as in other nymphalids, and hang straight down only after pupation. Ramos (1984) described the pre-pupa of *A. troglodyta borquenalis* as different from these four species—it is the only one that curls vertically.

In addition to the species discussed above, the early stages of *Anaea euryphyle confusa* Hall (Muyschondt 1974b) also are similar to those of *A. ryphea*. Both use species of *Croton*, and the eggs and larvae are similar. There are slight differences in head sculpturing and body color of the larvae, and in color and shape of the adult's wings.

The life history information presented above on *A. ryphea* was collected during extensive field observations. The animals in my study were allowed to remain under natural conditions in contrast to the laboratory conditions of the other studies cited above. This is one of the reasons for the dramatic decrease in numbers of observations from one instar to the next, which more accurately reflects the fate of natural populations in the field. Only the pre-pupa and pupa stages had to be observed in the laboratory because fifth instar larvae would have been lost when they left their plants to pupate. No pupae were ever found on or near *C. floribundus* in the field.

Variations in rearing conditions can affect the ultimate form of the adult in species with seasonal forms. This was studied by Riley (1981, 1989) in *A. andria*. So far, no seasonal variation has been observed in *A. ryphea* in the field, although males exhibit considerable variation in the color and shape of the wings.

←

### Herbivory and Associated Fauna

*Anaea ryphea* larvae seldom were seen eating the lowest leaves (old and damaged), and they never fed on apical leaves. Other herbivores also were observed on the intermediate portions of the plants. One species of cricket (Orthoptera: Gryllidae) ate patches from the leaves giving them the aspect of lace; one species of beetle (Coleoptera: Chrysomelidae) was observed eating the petiole; and one species of true bug (Hemiptera) appeared to be feeding on the petiole. Larvae of *Hypna clytemnestra* Cramer (Nymphalidae) are common on *Croton floribundus*, frequently outcompeting *A. ryphea* with their ability to defoliate small plants. There also is a species of aphid (Homoptera: Aphidae) that uses *C. floribundus*. Individuals aggregate on the undersides of leaves, and as a result, the upperside becomes dotted with white spots.

A leaf-mining microlepidopteran was taken to the laboratory for rearing, but all individuals died before pupation; hence, identification was not possible. The mine follows the edge of the leaf and when that area is used, the larva turns toward the central part of the leaf following the central vein, never crossing it. *Pheidole* ants (Hymenoptera: Formicidae) were seen predating upon eggs of *A. ryphea* ( $n = 10$ ), but were never observed interacting with the larvae.

In addition to those species mentioned above, a variety of other insects and spiders were seen regularly on *C. floribundus*, but not feeding on it. Some individuals of *C. floribundus* produce globs of a translucent gum, usually close to the apical leaves, that perhaps serve as a mechanical defense against some herbivores.

The practice of leaving the midvein and secondary veins intact, as exhibited by *A. ryphea*, appears to represent a feeding strategy described for other species of Lepidoptera (Compton 1987); and differs from the strategy of those species that cut the midvein to prevent toxins from getting to the portion of the leaf to be consumed. The former strategy allows the larvae of *A. ryphea* to avoid contact with the latex that *C. floribundus* produces, which suggests that they are incapable of detoxifying or storing high concentrations of this substance. *Hypna clytemnestra* and the leaf-mining microlepidoptera reported from *C. floribundus* also avoid the midvein, although the former may eat secondary veins. This type of behavior has been interpreted as an important step toward a disguise for these larvae (Hingston 1932) which add pieces of leaves and fecula to the midvein to improve the resemblance of the substrate to their body (Fig. 4). Such a behavior may reduce the level of predation.

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## METHODS FOR SEXING LEPIDOPTERA LARVAE USING EXTERNAL MORPHOLOGY

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**Abstract.** This paper describes a method for determining the sex of larval Lepidoptera using external morphology. This method, previously developed by others but published in journals with limited distribution, uses sex-specific pits located ventrally on the 8th and 9th abdominal segments. This paper also describes a new technique for clearing and staining newly hatched larvae so that these sex-specific pits can be identified readily. Finally, this paper extends the applicability of this method to four other species in three butterfly families (Papilionidae, Nymphalidae, and Pieridae).

**Additional key words:** sex determination, larval morphology.

The ability to sex live Lepidoptera larvae would allow for novel experiments on sex-specific differences in behavior, physiology, and development, as well as hormonal and metabolite assays, to name a few. Determination of sex ratio and sex-specific mortality typically has been limited to those larval stages where sex can be determined by dissection. Yet in most species gonad differentiation does not occur until at least the third instar, and in some species such as *Papilio zelicaon* Lucas (Papilionidae), even last instar larvae are impossible to sex by examining the gonads. Moreover, sexing by dissection necessarily involves sacrificing the animals—thereby precluding any further study of these individuals.

This paper describes a method of wide application for sexing Lepidoptera larvae using external morphology. It was developed by others but published in journals with limited distribution (Joseph & Karnavar 1991, Lavenseau 1982, Muraleedharan & Muraleedharan 1989, Stehr & Cook 1968) and seems to be little known or used. Aside from *Pieris rapae* L. (Pieridae), this method has been tested previously only in the moth families Psychidae, Pyralidae, Notodonidae, Lymantridae, Noctuidae, Arctiidae, and Attacidae (Stehr & Cook 1968, Lavenseau 1982, Muraleedharan & Muraleedharan 1989, Joseph & Karnavar 1991).

Larvae can be sexed live once they are large enough, typically at least 5 mm in length, to allow one to clearly see the last four abdominal segments under a dissecting microscope. All instars of preserved larvae can be sexed. This paper extends the applicability of this method to four other species within three butterfly families. It also presents a new technique for clearing and staining very young preserved larvae, including first instars, so that this method can be used to determine their sex.

## MATERIALS AND METHODS

Fifth instar larvae of *Eucheira socialis* Westwood (Pieridae), *Battus philenor* Linnaeus (Papilionidae), *Junonia coenia* Hübner (Nymphalidae), and *Papilio zelicaon* were sexed readily by examining the 8th and 9th abdominal segments using a Wild dissecting microscope. I first sexed individuals using external morphology, then dissected and sexed the same individuals by examining their gonads. I examined at least 10 larvae, five of each sex, from each of the four species of butterflies. All sex determinations were confirmed by dissection for all species except *Papilio zelicaon* where gonadal differentiation was insufficient in fifth instar larvae to determine sex. For this species, I sexed individuals by external morphology, then reared them out and sexed them as adults.

First instar larvae of *E. socialis* preserved in a 1:3 part mixture of glacial acetic acid and methanol were placed in a petri dish with glycerin and acetic acid (1:4). Petri dishes with larvae were put into larger covered petri dishes to prevent excessive evaporation, then placed in an oven at 60°C for two hours. Petri dishes were removed from the oven and left at room temperature for 22 hours. The front half of each larva was removed with forceps. The remaining rear half was placed in Hoyer's medium, prepared using the protocol in Ashburner (1989), and then incubated in an oven at 37°C for 18 hours. Slides were prepared with Hoyer's as the mounting medium with larvae oriented ventral surface up. I viewed slides under epi-illumination using a plan 16 objective, 50W mercury bulb, cross polars, a heat filter, and a green interference filter. Slides prepared in this manner should be useful for several weeks, but eventually will degrade.

## RESULTS

Sex determined by external morphology was confirmed by dissection or sexing adults in all but one larva. The only erroneously sexed larva, a *P. zelicaon*, belonged to the species most difficult to sex because larvae were light in color and the pits lacked contrasting coloration.

Sex-specific pits were clearly visible on the ventral surface of larvae (Figs. 1 and 2). Males were characterized by having one central pit on the 9th abdominal segment. Females had four pits, two located on each of the 8th and 9th abdominal segments.

For larvae requiring clearing and staining, the time necessary for the initial treatment of glycerin and acetic acid and for the Hoyer's treatment probably will depend upon the particular characteristics of the larvae to be examined. Some species may require more complete clearing and longer incubation times at perhaps greater temperatures, while others may not require clearing at all. The best preparations of

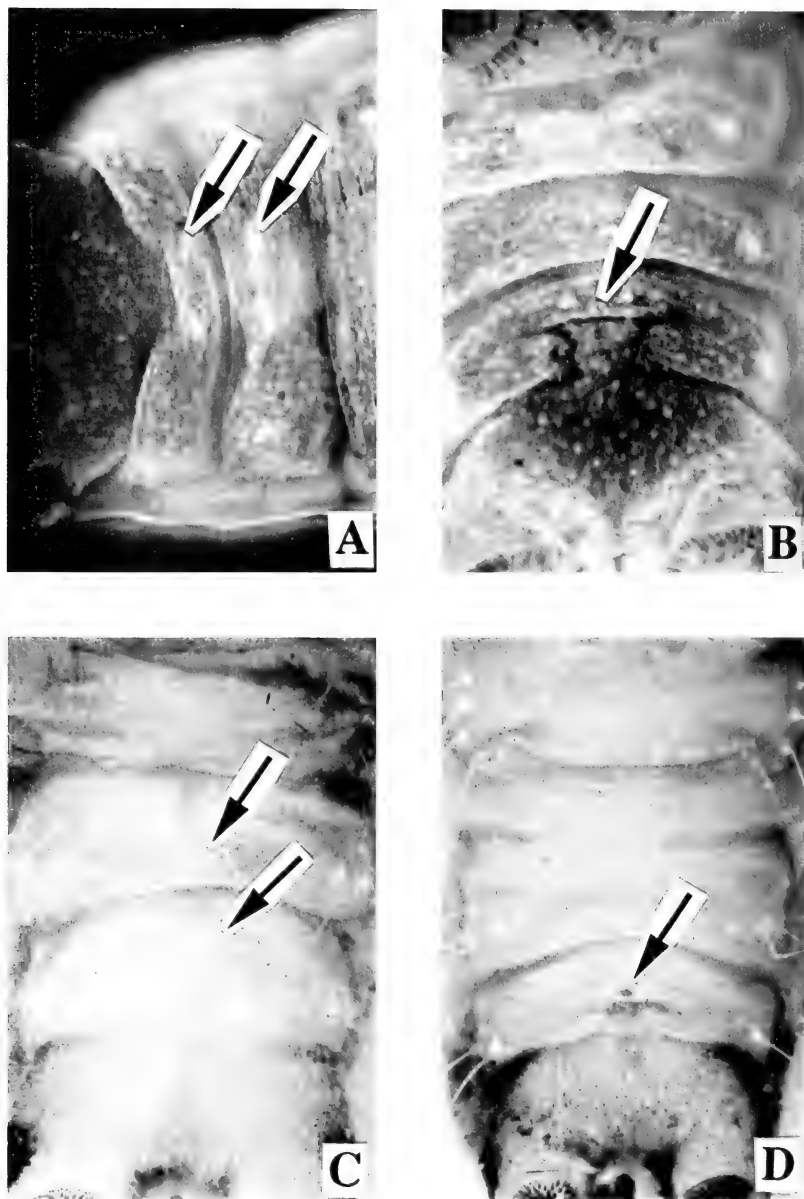


FIG. 1. First instar *Eucheira socialis* (Pieridae). (A) female (160 $\times$ ) with four pits, and (B) male (160 $\times$ ) with one pit; pits indicated by arrows. See text for details on microscope settings. Fifth instar *E. socialis*. (C) female (16 $\times$ ) with four pits, and (D) male (16 $\times$ ) with one pit. All animals in the photos are preserved and, except (A), are oriented with the posterior end downward.

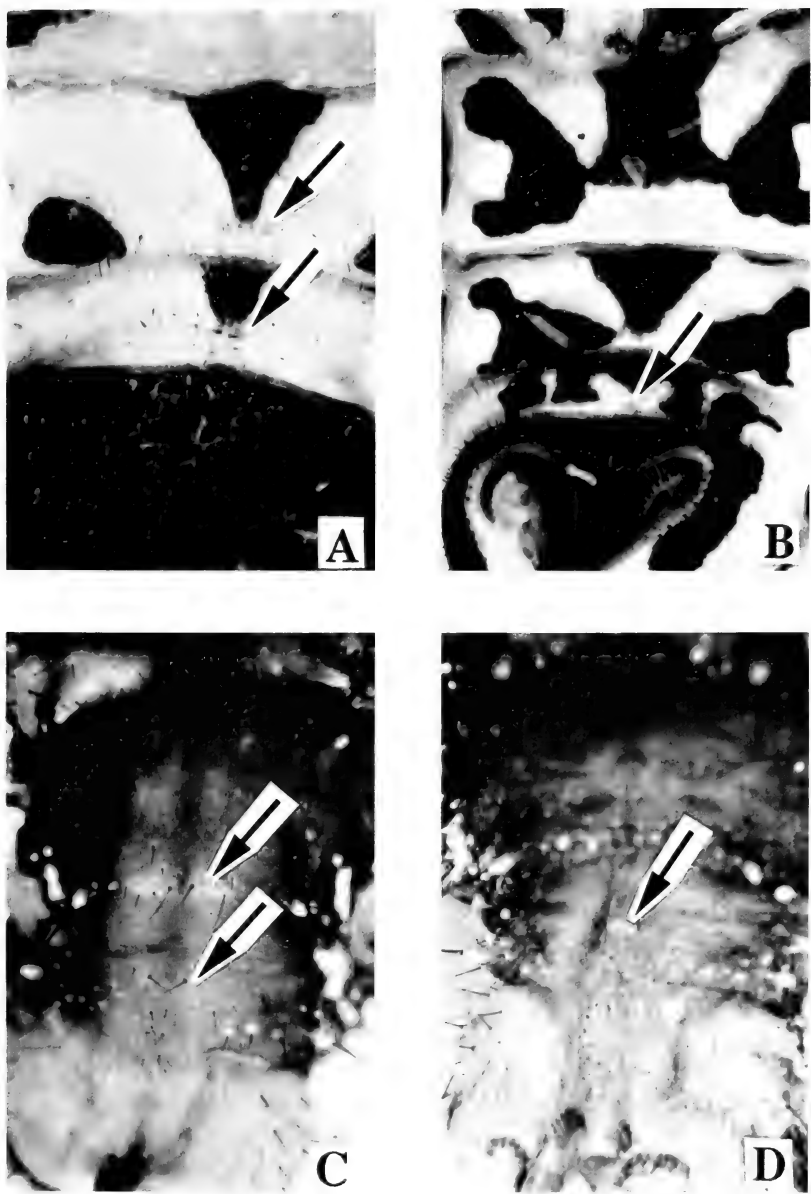


FIG. 2. *Papilio zelicaon* (Papilionidae) (A) female (20 $\times$ ), (B) male (16 $\times$ ); *Junonia coenia* (Nymphalidae) (C) female (18 $\times$ ), (D) male (20 $\times$ ). All animals in the photos are preserved and oriented with the posterior end downward.

first instar *E. socialis* were those with partial clearing; second instars could be sexed readily without clearing but needed the additional magnification of the compound microscope and epi-illumination.

### DISCUSSION

Depending upon age and/or species, it was sometimes easier to identify one sex or the other. In *E. socialis*, female second to fourth instars were readily identified because the four pits were surrounded by lighter colored halos, while the male pits were relatively difficult to discern. Fifth and sixth instar male *E. socialis* were quickly identified because the pit typically was darkened while the female pits were less distinctive. In contrast, female *J. coenia* were much more distinctive than the males even though only one pair of pits in the female was predictably discernable. Female *P. zelicaon* also were easier to sex than males, but both were sometimes difficult because these larvae are very light in color, and the pits lacked contrasting coloration.

Lavenseau (1982) sexed first instars by searching for abdominal pits on larvae using scanning electron microscopy. This technique requires relatively elaborate protocol for preparing larvae. The technique for clearing and staining first instar larvae described here requires only a microscope capable of epi-illumination. The procedure used here for clearing larvae using Hoyer's medium is used in our introductory embryology course at the University of California at Davis to study cuticular mutations in *Drosophila* embryos; hence, it is simple enough to be done successfully by the inexperienced.

Two other techniques have been published to sex larvae with undifferentiated gonads which do not use sex-specific abdominal pits. The nuclei of many species of animals are known to contain darkly staining bodies which correlate with the presence of the Y chromosome (Smith 1945a, 1945b, Ennis 1976, Traut & Scholz 1978, Clarke 1984). Clarke (1984) identified the sex of living larvae by removing a proleg and scraping enough tissue for preparations which stain heteropycnotic bodies. However, these heteropycnotic bodies are not always evident in females in some species of Lepidoptera, or rarely, they are seen in both sexes (Traut & Mosbacher 1968, Ennis 1976, Traut 1976).

Seiler (1964), in a study on intersexes in a moth, *Solenobia triquetrella* F. R. (Psychidae), sexed larvae with undifferentiated gonads by following the gonoducts. In females, the gonoducts terminate at the 7th abdominal segment, and in males, they terminate at the 9th abdominal segment where they connect to the ectodermal anlage of the male copulation organ (the Organ of Herold). Newly hatched larvae were sexed by the presence or absence of the Organ of Herold. However,



this method cannot be used on living larvae no matter how mature, and I found the dissections tedious and difficult to perform.

#### ACKNOWLEDGMENTS

I thank Mark Camara and Sherri Graves for donating live larvae. Adam Porter lent me Stehr and Cook's publication which first introduced me to this method. Peter Armstrong made possible the photos taken through the epi-illuminating microscope and Judy Nelson provided assistance in photographing the fifth instars. Jeanette Natzle suggested using the clearing method for the first instars and she provided the Hoyer's medium.

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## GENERAL NOTES

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### SOMATIC MOSAICISM IN *MANIOLA JURTINA* (NYMPHALIDAE: SATYRINAE)

**Additional key words:** bilateral size asymmetry.

Spontaneously appearing perfectly or nearly perfectly bilaterally differentiated, but non-gynandrous, individuals are known chiefly in the silkworm (*Bombyx mori* L., Bombycidae), fruit fly (*Drosophila melanogaster* L., Drosophilidae), and honeybee (*Apis mellifera* L., Apidae), and in some domesticated vertebrates. Selected examples from butterflies include female *Papilio polytes* L. (Papilionidae) with one side of the sex-limited f. "romulus" Cramer and the opposite side of male-like f. "cyrus" Fabricius (Ollenbach 1930); half black/half yellow morph females of *Papilio glaucus* L. (Papilionidae) (for a review see Clarke & Clarke 1983, Scriber & Evans 1988); and male *Apatura ilia* (Den. & Schiff.) (Nymphalidae) with one side of f. "silvia" Cabeau (Cockayne 1935). Apparently, asymmetries in butterflies involve mainly differences in wing pattern and coloration, and to a lesser extent, the shape and size of the wings. Some may represent cases of wing homoeosis (for a review see Sibatani 1980, 1983a, b).

The teratology described herein concerns exclusively the size of body halves. The example was found in the field stock of two thousand specimens of the meadow brown, *Maniola jurtina* (L.) (Nymphalidae: Satyrinae), collected in July 1968 near Jarocin, Poland (51°58'N, 17°29'E), among lowland herb communities of the class Molinio-Arrhenatheretea. The aberrant specimen is a female (not a latent gynander) with the right part of the body distinctly smaller than the left, exhibiting ca. 8% linear difference (Fig. 1). The halving proceeds about the entire median line, equally affecting all structures of the right side of the head (e.g., palpus, antenna, compound eye), thorax (e.g., legs, wings with their scales and markings), and abdomen. For instance, the length of the left forewing (from



FIG. 1. Bipartite mosaic female of *M. jurtina*.

base of costa to apex) is 23 mm, whereas that of the right is 21 mm (usual wing length in Polish populations is 23–25 mm).

So far as I am aware, this represents the most obvious case of bilateral asymmetry in expression of insect body size, uncoupled with any other conspicuous asymmetric deviation, reported in the literature. The left-right difference in size is much more pronounced than that in bilateral gynandromorphs of *M. jurtina* figured by Barrington (1992), Albrecht (1993), or Eitschberger (1993).

As to their origin, "half-siders" in diploids are believed to result from point mutations, rearrangements, or malsegregation of chromosomes giving diversity at the first division of the zygote nucleus, or from double fertilization of a binucleate egg. In butterflies, mosaics thought to arise by polyspermy generally are gynandromorphic (preliminary separation of sister chromatids in meiosis) (Blanchard & Descimon 1988). Instead, non-disjunction of the homologues (i.e., XY/XO) recently has been proposed to be involved in appearance of the previously mentioned aberrations of *P. glaucus* (Clarke & Clarke 1983, Scriber & Evans 1988). Comparative analysis of chromosomal DNA derived from the two halves of the aberrant specimens like that reported here may help in mapping loci that affect insect growth.

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HYMENOPTEROUS PARASITOIDS OF *DISMORPHIA SPIO*  
(PIERIDAE: DISMORPHIINAE)

**Additional key words:** *Trichospilus*, *Trichogramma*, Puerto Rico.

The following presents records of parasitoids of *Dismorphia spio* (Godart) reared from eggs and pupae collected during 1984–1986 in Barrio Guaonico, Utuado, Puerto Rico.

During the study of the biology and natural history of *D. spio* (Torres Bauzá 1991a), I collected five eggs parasitized by *Trichogramma* sp. (Trichogrammatidae). This represents a parasitization rate of about 11% (n = 47) among the natural population. From each egg, up to six wasps emerged four to six days after collection. In Puerto Rico, *Trichogramma* sp. have been reported from eggs of *Diatraea saccharalis* (F.) (Pyralidae), *Etiella zinckenella* (Treitschke) (Pyralidae), *Psara periusalis* (Walker) (Pyralidae), *Calpododes ethlius* (Cramer) (Hesperiidae), and *Eurema portoricensis* (Dewitz) (Pieridae) (Wolcott 1951, Torres Bauzá 1991b).

A pupa of *D. spio* collected on *Inga vera* Willd. (Mimosoideae) hosted *Trichospilus diatraea* Cheriau & Margabandhu (Eulophidae). This represents a parasitization rate of about 1% (n = 84) among the natural population. Seventy wasps emerged from the pupa five days after collection. *Trichospilus diatraea* has been collected from *Spodoptera frugiperda* (Smith) (Noctuidae), *Epimecis detexta* (Walker) (Geometridae), *Trichoplusia ni* Hübner (Noctuidae), *Pseudoplusia includens* Walker (Noctuidae), *Diaphania hyalinata* (L.) (Pyralidae), and *Stenorrhages flegia* (Cramer) (Pyralidae) in Florida, Trinidad, and Barbados (Bennet & Alam 1985, Bennet et al. 1987). This is the first report of *T. diatraea* in Puerto Rico.

Representatives of the reared parasitoids are deposited in the entomological collection of the Agricultural Experimental Station, University of Puerto Rico, Mayaguez Campus at Río Piedras, Puerto Rico (lot number 90-10217).

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## OBITUARY

ALBERT SCHWARTZ (1923-1992)

The name Albert Schwartz is virtually synonymous with West Indian zoology. For nearly 40 years, Al devoted his life to the discovery, documentation, and description of butterflies, frogs, reptiles, birds, and mammals of the West Indian Islands. He probably was best known to lepidopterists for his book *The Butterflies of Hispaniola* and research on satyrid butterflies in the genus *Calisto*. Albert Schwartz died on Sunday, 18 October 1992 in a local hospital a few days after undergoing surgery for injuries sustained in a fall at his home in Miami, Florida.

Schwartz was born on 13 September 1923 in Cincinnati, Ohio. He received his B.S. (Psychology) in 1944 from the University of Cincinnati, his M.S. (Zoology) in 1946 from the University of Miami, and his Ph.D. in 1952 from the University of Michigan. His master's thesis topic was "Cestodes of sharks of the east coast of Florida" and doctoral dissertation topic was "Mammals of southern Florida and the upper Florida keys." Al had a broad interest in zoology, but even as a graduate student, was drawn towards work on faunal surveys and descriptive studies.

After completion of his doctorate, Al accepted a position in South Carolina as Curator of Vertebrate Zoology at the Charleston Museum. In 1956, he moved to Reading, Pennsylvania and taught in the Biology Department of Albright College. Later he returned to Florida where he spent most of his professional career (1967-1988) teaching at Miami-Dade Community College. Because this was a non-research position, Al conducted his studies entirely on his own time. Even after retirement, Al jealously guarded his free time and carefully structured his life to maximize the time devoted to research on West Indian fauna and other favorite pursuits. Al was a gifted pianist, loved opera, and composed music as a hobby. A life-long bachelor, he enjoyed entertaining close friends but generally shunned large gatherings.

Al's West Indian field studies started in 1954 on Cuba, which remained his favorite island despite the inaccessibility to outside researchers in later years. In the late 1970s, having already accomplished many of his goals for surveying the herpetological fauna of the islands, Al began working on Lepidoptera and quickly realized that he could make significant contributions in this area of study. By the time of Al's death, insect cabinets filled two bedrooms of his home, and shelving lined most of the wall space in living and dining rooms to house the oversized drawers with his butterfly collection. The collection includes



FIG. 1. Albert Schwartz in the early 1970s. Photo courtesy of M. H. Strahm.

more than 28,500 specimens primarily from the West Indies and Florida, with detailed locality data and documentation.

The fauna of the islands captivated Al Schwartz and the scientific output which resulted was enormous. He published 230 papers (some 5,100 pages) on West Indian zoology, including descriptions for three new species of bats, nearly two dozen species of butterflies, 80 species of amphibians and reptiles, and about 279 subspecies of frogs, lizards, and snakes. At the time of his death, he was collaborating on several papers dealing with West Indian mammals, amphibians and reptiles, and Lepidoptera (including a color atlas of Hispaniolan butterflies with Fernando González).

Students often accompanied Al in the field, and he also subsidized fieldwork for many of his collaborators. This became especially critical in his later years as chronic arthritis left Al increasingly incapacitated

and he had to rely on others to collect additional specimens and data. I came to know Al through my co-workers, Robert W. and Rose M. Henderson. Bob is a herpetologist and Rose an artist with the Milwaukee Public Museum. They both collaborated with Al on various projects and developed a warm friendship. While I never had the pleasure of meeting Al, I thoroughly enjoyed our phone conversations. Al had a wonderful sense of humor. He was a very open and direct person, and a great teacher, always encouraging and stimulating new ideas. Al Schwartz enriched the lives of numerous other lepidopterists, and his research legacy will serve as an inspiration for those studying the fauna of the West Indies for many years to come.

As stipulated in his will, the Schwartz butterfly collection has been donated to the Milwaukee Public Museum by Michael H. Strahm, friend and former student of Al Schwartz, and executor of his estate. I owe special thanks to Bob Henderson for introducing me to Al, and for sharing fond remembrances and specific details about Al's life for this article.

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#### LEPIDOPTERA PUBLICATIONS BY ALBERT SCHWARTZ

##### 1980

1. (with W. W. Sommer) A new species of *Atlantea* (Nymphalidae) from Hispaniola, West Indies. Bull. Allyn Mus. 58:1-4.
2. Deforestacion y Rhopalocera una comparacion en la recoleccion de mariposas entre República Dominicana y Haiti. Nat. Postal 30/80: 1-3.

##### 1982

3. (with C. J. Jimenez) The butterflies of Montserrat, West Indies. Bull. Allyn Mus. 66:1-18.
4. Variation in Hispaniolan *Greta diaphana* (Ithomiidae). Bull. Allyn Mus. 69:1-10.

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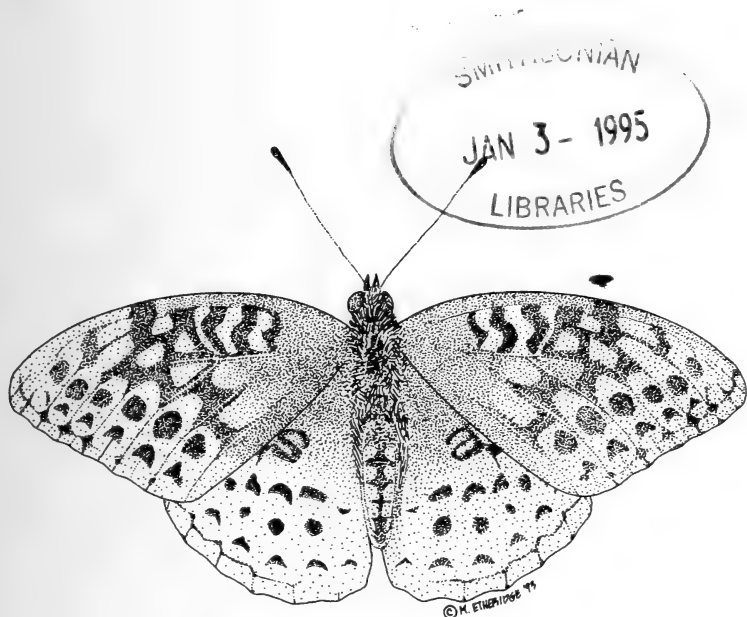
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**Cover illustration:** The largest North American silverspot, the great spangled fritillary, *Speyeria cybele* (Fabricius) (Nymphalidae). Original drawing by Mark Etheridge, 9422 Fairleigh Court, Burke, Virginia 22015.

# JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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## GENITALIA AT THE GENERIC LEVEL: ATRYTONE RESTRICTED, ANATRYTONE RESURRECTED, NEW GENUS QUASIMELLANA—AND YES! WE HAVE NO MELLANAS (HESPERIIDAE)

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**ABSTRACT.** Some prior opinion notwithstanding, both male and female genitalia are exceedingly valuable in delimiting genera of skippers and in grouping species within genera. Even such small genitalic parts as the cornutus and juxta of the male can have value out of all proportion to their size.

The New World genera *Atrytone* Scudder and *Mellana* Hayward are polyphyletic. *Atrytone* genitally sorts out into (1) *Atrytone*, with the one species *Atrytone arogos* (Boisduval & Leconte) from the central and eastern United States, and (2) the old synonym *Anatrytone* Dyar, with eight species, ranging from southern Canada to Argentina. Half of these species were in *Mellana* (and in synonymy besides); and they include the type species of *Mellana*, which thus becomes a new synonym of *Anatrytone*. For much of what was in *Mellana*, plus five new species, I genitally define the **new genus Quasimellana**, with a total of 24 species, ranging from the far southern United States to northern Argentina. Despite superficial similarities between some species, *Anatrytone* and *Quasimellana* are not closely related.

All names in *Anatrytone*, except those of the type species *Anatrytone logan* (Edwards) and the new species *A. sarah*, and all names in *Quasimellana*, except those of the new species *Quasimellana siblinga*, *Q. antipazina*, *Q. andersoni*, *Q. imperfida*, and *Q. mielkei*, are new combinations. The type species of *Quasimellana* is *Q. mexicana* (Bell). In the following lists, eight new synonyms appear in brackets.

I genitally define two species groups in *Anatrytone*, each of which (a) ranges widely (Canada to Argentina/Mexico to Argentina) and (b) comprises four species that tend to replace one another geographically: (1) the *logan* group with the North American *logan* subgroup comprising *Anatrytone logan* (Edwards) and *A. mazai* (Freeman) and the South American *barbara* subgroup comprising *A. barbara* (Williams & Bell) and *A. flavens* (Hayward); and (2) the compact *mella* group comprising *A. potosiensis* (Freeman), *A. mella* (Godman), *A. sarah* n. sp., and *A. perfida* (Möschler) [= *gladolis* (Dyar)].

I genitally define three species groups in *Quasimellana*: (1) the *eulogius* group (southern United States to Brazil and Paraguay, but mainly North American) with the five species *Q. mexicana* (Bell), *Q. eulogius* (Plötz) [= *agnesae* (Bell), = *oaxaca* (Freeman)], *Q. siblinga* n. sp., *Q. balsa* (Bell) [= *balsa freemani* (Steinhauser)], and *Q. mulleri* (Bell); (2) the *sethos* group (Mexico to Bolivia and Brazil, and equally North and South American) with the 12 species *Q. aurora* (Bell) [= *tecla* (Steinhauser)], *Q. nayana* (Bell) [= *tamana* (Steinhauser)], *Q. noka* (Evans), *Q. pazina* (Evans), *Q. antipazina* n. sp., *Q. sista* (Evans),

*Q. andersoni* n. sp., *Q. sethos* (Mabille), *Q. myron* (Godman), *Q. verba* (Evans), *Q. inconspicua* (Hayward), and *Q. angra* (Evans); and (3) the *nicomedes* group (Mexico to Argentina, but mainly South American) with the seven species *Q. amicus* (Bell), *Q. fieldi* (Bell) [= *montezuma* (Freeman)], *Q. nicomedes* (Mabille) [= *monica* (Plötz)], *Q. imperfida* n. sp., *Q. mielkei* n. sp., *Q. meridiani* (Hayward), and *Q. pandora* (Hayward).

Four species put in *Mellana* by Evans belong neither in *Quasimellana* nor in *Anatrytone*: *gala* Godman, *helva* Möschler, *rivula* Plötz, and *clavus* Erichson, which is the differentiate of *Wallengrenia* currently going by the junior name *Wallengrenia otho curassavica* (Snellen).

**Additional key words:** systematics, species groups and sister species, New World, geographic distribution, *Wallengrenia*.

Genitalia are the best means to an end—for the holder, of course, but also, at quite another level, for the thoughtful beholder. Long exploited for separating species from one another, genitalia are just as good for pulling related species together in higher groups like genera.

Although Scudder and Burgess (1870, plus later work summarized in Scudder 1889) and Godman and Salvin (1879–1901) were way ahead of their time because they examined and illustrated the male genitalia of many of the skipper butterflies that they treated, they erred by placing species with similar genitalia in different genera and species with disparate genitalia in the same genus. For example, the twelve species of *Atrytone* whose genitalia grace plate 94 in Godman and Salvin actually belong to five distinct genera.

In North America, illustration of skipper genitalia continued with Barnes and McDunnough (1912), Skinner (1914), and especially Skinner and Williams (1922, 1923a, 1923b, 1924a, 1924b, 1924c) who figured the males of almost all the species then known from north of Mexico. When Lindsey, Bell, and Williams in 1931 updated Lindsey's 1921 treatment of this fauna, they incorporated the Skinner and Williams figures.

An overly guarded paragraph in Lindsey (1921:11) on the taxonomic uses of genitalia reappeared nearly verbatim in the collaborative revision (Lindsey et al. 1931:10), but with a couple of addenda (here set in italics):

The genitalia, especially in the males, are of great value in making specific identifications and similarity of genitalic structure often affords an index of generic relationship. We have found several apparent contradictions of the latter statement and are therefore inclined to use the principle cautiously until more is known about the skippers, but still we hesitate to include in the same genus species whose genitalia are of widely different forms *unless other structures indicate close relationship. Genitalia are obviously more erratic in their variation than other structures.*

These italic afterthoughts took a huge leap backward.



Though it soon became standard, in this country and abroad, to illustrate male genitalia in descriptions of new skipper species, the enormous store of information in published tails was—and is—relatively untapped. Authors would dutifully show a new tail but often say little or nothing about it, even with respect to the species from which it came, much less compare it critically with others for clues to higher affinities. Despite exploitation by Barnes and McDunnough (1912) in megathymines, female genitalia were mostly ignored until MacNeill (1964) in *Hesperia* and Burns (1964) in *Erynnis* made heavy, comparative use of them. Female genitalia can be as helpful as those of the male.

We are still seduced by outward appearance: *simius* Edwards looks like an *Amblyscirtes*—but its genitalia, in both sexes, spurn the *Amblyscirtes* mold; reexamination of “other structures” shows that the palpi and especially the antennal apiculus also deviate significantly; and *simius* must go elsewhere (Burns 1990). Again, *nabokovi* Bell & Comstock (1948) superficially looked like an *Atalopedes* to its describers, who routinely figured the tail of the male—but those genitalia, in both sexes, are unabashed variations on the *Hesperia* (not the *Atalopedes*) theme; the stigma, too, comes straight from *Hesperia*; and that is where *nabokovi* goes (Burns 1987, 1989). Despite appearances (and convention), genitalia clearly show that *snowi* (Edwards) belongs in *Paratrytone* rather than *Ochlodes* and that two-thirds of the species currently in *Paratrytone* belong somewhere else—mostly with the non-marsh-dwelling species of *Poanes*, which, in turn, harbor a pair of outwardly acceptable genitalic misfits (Burns 1992).

Granted, genitalia are far more difficult, tedious, and time-consuming to study and compare rigorously. But their morphologic complexity in skippers yields a wealth of potential characters (often enriched through asymmetry). Being hidden and serving quite other functions, they escape many of the pressures bombarding the external, visual phenotype and tend to reflect relationship better than facies.

During the last eight years I have been genitally reviewing nearctic hesperiine skippers, a relatively well-studied fauna whose long-stable genera seem to be gaining authority—yea, rigidity—through constant repetition in a spate of state, provincial, seminational, and national butterfly books and checklists (e.g., Harris 1972, Irwin & Downey 1973, Hooper 1973, Shapiro 1974, MacNeill 1975, Dornfeld 1980, Stanford 1981, Pyle 1981, Miller & Brown 1981, 1983, Opler & Krizek 1984, Scott 1986, Tilden & Smith 1986, Heitzman & Heitzman 1987, Shull 1987, Klassen et al. 1989, Bailowitz & Brock 1991, Opler & Malikul 1992, Iftner et al. 1992). Unfortunately, as I have intimated, our genera are a mess. Problems generally spread into the neotropics, where they

ramify—but where specimens and data are so much scarcer that sophisticated generic revision dealing fully with all relevant species is not practical. Even if it were, I am finding mistakes at the generic level too rapidly to give each affected species anything like the time and attention I have lavished on pairs of close and confusing differentiates within *Erynnis*, *Celotes*, *Atrytonopsis*, *Autochton*, *Wallengrenia*, and *Pyrgus* (Burns 1964, 1974, 1983, 1984, 1985, unpublished). Such detail is dispensable because problems of grouping species in genera are different from problems of delimiting species and analyzing speciation.

I aim here and in some related papers (e.g., Burns 1992, 1994) to redefine certain genera strictly by means of genitalia. Many short generic descriptions—including those of Evans (1955)—that omit genitalic characters really fail to characterize. Some recent long descriptions manage to drown a few useful genitalic observations in an indiscriminate sea. At the very least, my corrected generic limits will lead to better evolutionary, ecologic, ethologic, and biogeographic generalizations about American hesperiines.

Since my examination of their genitalia has shown that some type specimens are not what others thought, I have had to make some jolting changes in nomenclature. The abbreviations I use in citing museums are spelled out at the beginning of Acknowledgments (p. 334). All X-rated genitalia dissections are mine.

*Atrytone* Scudder vis-à-vis *Anatrytone* Dyar  
(Figs. 1–3, 16, 17)      (Figs. 4–15, 18–27, 83–86)

Scudder (1872) “defined” his new genus *Atrytone* merely by designating *Hesperia iowa* Scudder (= *Hesperia arogos* Boisduval & Leconte) type species and by including three other species originally described in *Hesperia*: *logan* Edwards, *conspicua* Edwards, and *zabulon* Boisduval & Leconte. Because this largely nearctic assemblage is heterogeneous, interpretation of *Atrytone* varied. Over the next eight decades, chiefly Godman, Dyar, Williams, Bell, and Hayward described many and various neotropical species in *Atrytone*. Hayward (1948) made one of them, *mella* Godman, the type of his monotypic new genus *Mellana*. Meanwhile, Barnes and McDunnough (1916) removed *zabulon* (plus a few of its congeners) to *Poanes*; and, eventually, Evans (1955) removed *conspicua* (plus what by then were seven related congeners) to *Euphyes* and all of the modern neotropical species of *Atrytone* to *Mellana*, leaving *Atrytone* with just two nearctic species from the eastern and central United States and adjacent Canada: *arogos* and *logan*. Later, Freeman (1969) described two new species of *Atrytone* from Mexico: *mazai* and *potosiensis*.

Dyar (1905) “characterized” his heterogeneous new genus *Anatry-*

*tone* in four and a half lines of undiagnostic text, designated *Hesperia delaware* Edwards (= *Hesperia logan*) type species, and included also *lagus* Edwards (now considered a subspecies of *logan*), *vitellius* Fabricius (now in *Choranthus*), and, of all things, *arogos*—the type species of *Atrytone*! (Dyar placed in *Atrytone* four skippers congeneric with one another though not with *arogos*.) Skinner (1905) lost no time in pointing out this grand idiocy, and *Anatrytone* has been called a synonym of *Atrytone* ever since (e.g., Barnes & McDunnough 1916, Lindsey 1921, Lindsey et al. 1931, Evans 1955, dos Passos 1964, Miller & Brown 1981, 1983).

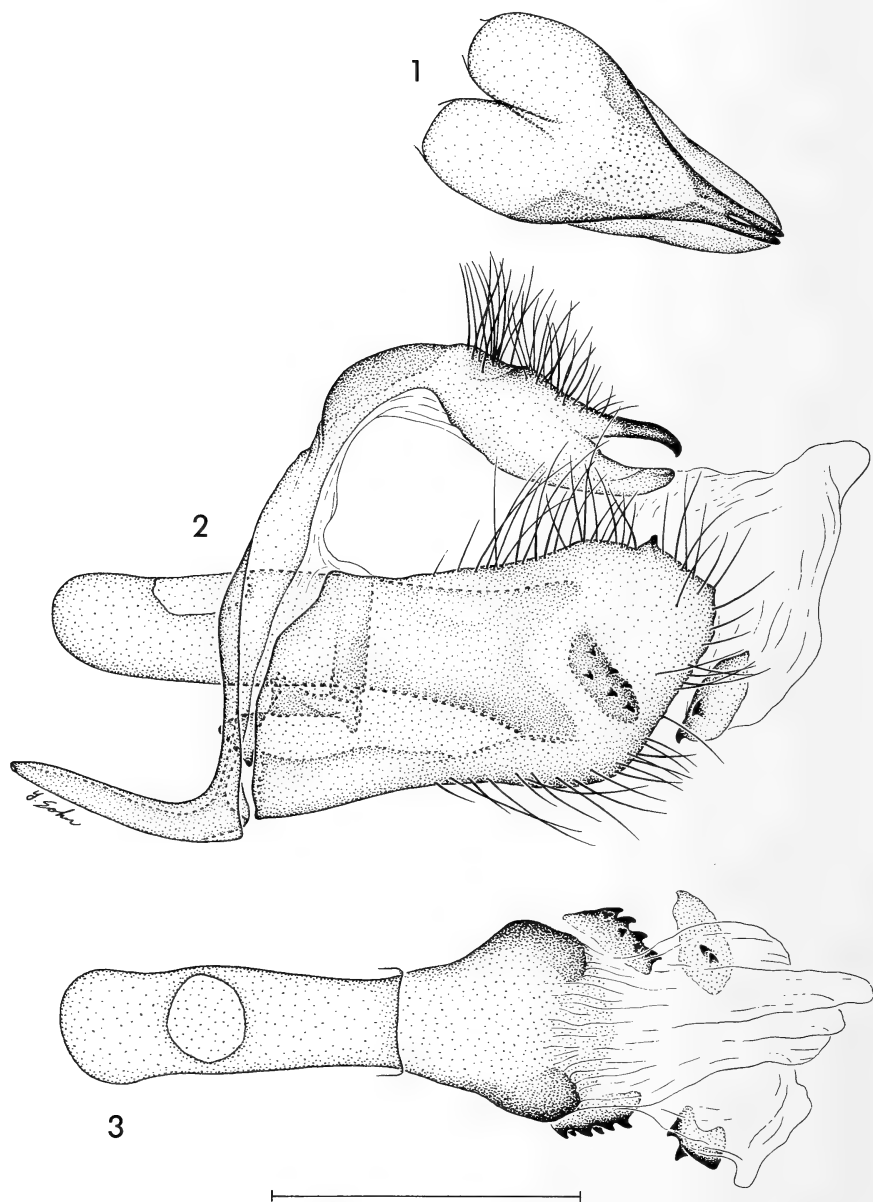
But the two genera do have different types, *arogos* and *logan*; and, as I demonstrated in great genitalic detail at the annual meetings of The Lepidopterists' Society in 1990 and 1991, these two fairly similar looking species (which have always been grouped—even by Dyar) really belong in separate genera. We must refer to *Atrytone arogos* and *Anatrytone logan*. Seizing mostly on differences in immature stages and life history, Scott (1992) reached the same conclusion.

For the record, I wish to emphasize that male tails of these skippers have been adequately shown in the past (though improperly read): *logan* by Scudder (1889:pl. 37, fig. 11) and, more completely, by Godman (1900:pl. 94, fig. 6); both *arogos* and *logan* by Skinner and Williams (1924a:figs. 12, 13—reprinted in Lindsey et al. 1931 on plates 27 and 28).

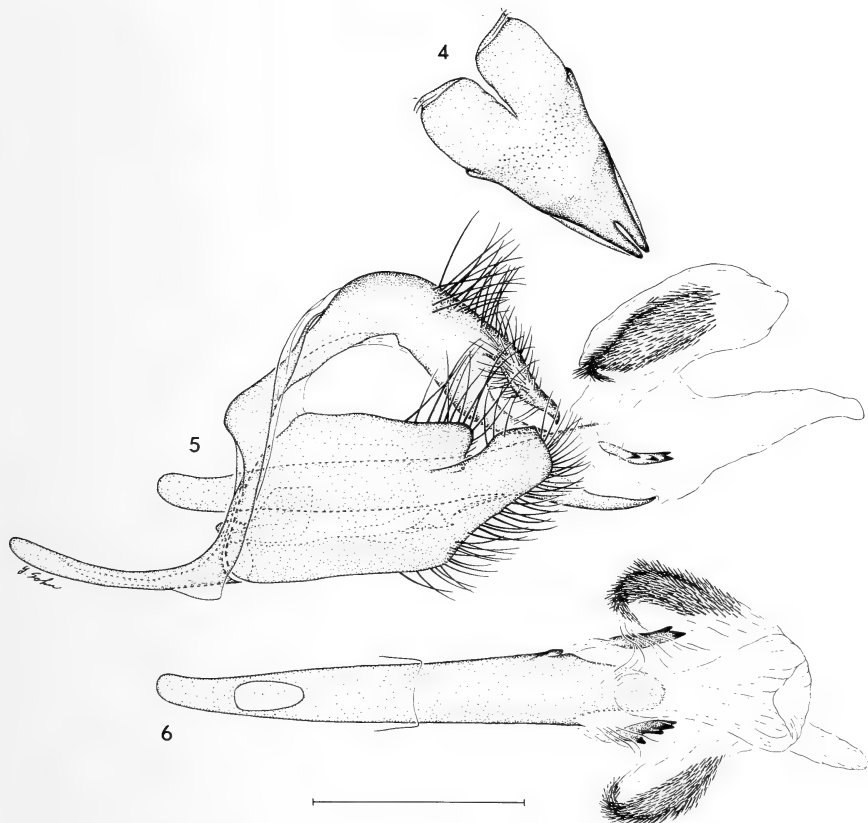
How do the genitalia of *Atrytone* and *Anatrytone* differ? Not with the “saccus longer” in *Anatrytone*, as claimed by Scott (1992:135).

An answer requires more than comparing the type species. Although, with the loss of *logan*, *Atrytone* is currently monotypic, *Anatrytone* is decidedly polytypic, containing not just *logan* and the above mentioned Freeman species, *mazai* and *potosiensis*, but five other species that collectively range from Mexico to Paraguay and Argentina. Evans (1955) put four of those species in *Mellana*—and in synonymy besides! Scott (1992:136) wrongly asserted “that based on adult morphology ‘*Atrytone*’ *potosiensis* Freem. obviously belongs to genus *Mellana potosiensis* new combination.” In characterizing *Anatrytone*, I have studied and compared the genitalia of all eight species, and have chosen to figure fully those of *potosiensis*, *barbara* Williams & Bell, and *flavens* Hayward, as well as *logan*, because they are as different from *logan* as any in the genus. However, in showing extremes of genitalic variation within *Anatrytone*, I am more interested in conveying a sense of the resemblance among the species than of the differences between them. Once this essential similarity is grasped, the larger and qualitatively different gap between *Anatrytone* and *Atrytone* should be obvious.

In males of *Atrytone* (Figs. 1–3), the valva is simple: its only em-



FIGS. 1-3. Male genitalia of *Atrytone arogos* from loess hills, 1460 ft (445 m), 4½ mi (7¼ km) SE Westfield, Plymouth County, Iowa, USA, 1 July 1980, J. M. Burns (genitalic dissection no. X-2569) (USNM). Scale = 1.0 mm. 1, Tegumen, uncus, and gnathos in dorsal view. 2, Complete genitalia (minus right valva), with vesica everted, in left lateral view. 3, Aedeagus, with vesica everted, in dorsal view.



FIGS. 4–6. Male genitalia of *Anatrityone logan* from loess hills, 1150–1300 ft (350–395 m), 2.8 mi (4.5 km) W Ticonic, T85N, R44W, sect. 18 and 19, Monona County, Iowa, USA, 2 July 1980, J. M. Burns (X-2567) (USNM). Scale = 1.0 mm. **4**, Tegumen, uncus, and gnathos in dorsal view. **5**, Complete genitalia (minus right valva), with vesica everted, in left lateral view. **6**, Aedeagus, with vesica everted, in dorsal view.

bellishment is a small, toothlike flange on the distal dorsal rim (Fig. 2). The tegumen/uncus, in lateral view (Fig. 2), is dorsally concave above the point at which the gnathos diverges, and, in dorsal view (Fig. 1), is unevenly tapered to an extremely delicate pair of uncus prongs so that much of the underlying gnathos shows. The aedeagus (Figs. 2, 3) is short (distinctly shorter than the rest of the intact genitalia), stout, and distally flared. The everted vesica (Figs. 2, 3), which is short, sports two pairs of rigid cornuti below—the pair at the distal end of the aedeagus with more teeth than the pair beyond it.

In males of *Anatrityone* (Figs. 4–15, 24–27), the valva is more complex: a large notch in the dorsal rim splits a prominent dorsodistal

extension from the body of the valva (Figs. 5, 8, 11, 14, 27); toward and at the base of this extension are modest medial protrusions (Figs. 5, 8, 11, 14). The tegumen/uncus, in lateral view (Figs. 5, 8, 11, 14, 27), is dorsally convex above the point at which the gnathos diverges, and, in dorsal view (Figs. 4, 7, 10, 13), is more or less evenly tapered to a heavier pair of uncus prongs so that most (Fig. 4) or all (Figs. 7, 10, 13) of the underlying gnathos is concealed. The aedeagus (Figs. 5, 6, 8, 9, 11, 12, 14, 15, 24–27) is nearly as long as, or longer than, the rest of the intact genitalia; and its floor is caudally prolonged. The everted vesica (Figs. 5, 6, 8, 9, 11, 12, 14, 15, 24–26), which is long, sports one pair of rigid cornuti below, near the caudally prolonged floor of the aedeagus, plus (in all species but *barbara* [Figs. 11, 12] and *flavens* [Figs. 14, 15]) a pair of flexible, spinulose cornuti above (which suggest scouring pads).

The female genitalia look more immediately distinct: they are shorter in *Atrytone* than in *Anatrytone*. In females of *Atrytone* (Figs. 16, 17), the lamella postvaginalis is short (in ventral view, wider than long) and arched dorsad (see lateral view); its posterior margin is usually well notched at the midline. The ductus bursae is short, almost uniformly wide, and well sclerotized, with many longitudinal wrinkles, especially dorsally. The adjacent, posterior part of the corpus bursae is lightly sclerotized, with more (chiefly longitudinal) wrinkles.

In females of *Anatrytone* (Figs. 18–21) other than *barbara* (Figs. 22, 23) and perhaps *flavens* (whose female I have not seen), peculiar, roughly linear sclerotization occurs midventrally in membrane between the ovipositor lobes, posterior and dorsal to the lamella postvaginalis and separate from it. The lamella postvaginalis itself (Figs. 18–23) is long (in ventral view, longer than wide) and ventrally about flat, with its lateral edges bent dorsad (see both ventral and lateral views); its posterior margin varies from outwardly rounded to shallowly notched at the midline. The ductus bursae—though ranging from short to long and from well to poorly sclerotized—reflects a basic pattern that involves some tapering toward the ostium bursae (Figs. 18, 20, 22), some dorsal concavity (Figs. 19, 21, 23), and some tendency for its roof to become membranous anteriorly where it meets the corpus bursae. The corpus bursae is entirely membranous.

#### THE SPECIES OF *ANATRYTONE* (INCLUDING THE TYPE OF *MELLANA*)

##### The *logan* Group

(Figs. 4–6, 10–15, 18, 19, 22, 23)

*Anatrytone logan* is the northernmost member of a loose, four-species group extending from southern Canada to Peru, Brazil, and northern Argentina.

In males of the *logan* group, the saccus is long (Figs. 5, 11, 14); titillators are totally absent (Figs. 12, 15) or, in about half the individuals of *logan*, present in rudimentary form on just the right side of the aedeagus (Fig. 6); the rigid cornuti are more or less linear and long and parallel with the caudal prolongation of the aedeagal floor so as to suggest dorsolateral extensions of the aedeagal roof (Figs. 5, 6, 11, 12, 14, 15); and the valvae are usually low (Figs. 11, 14) to medium (Fig. 5) in height.

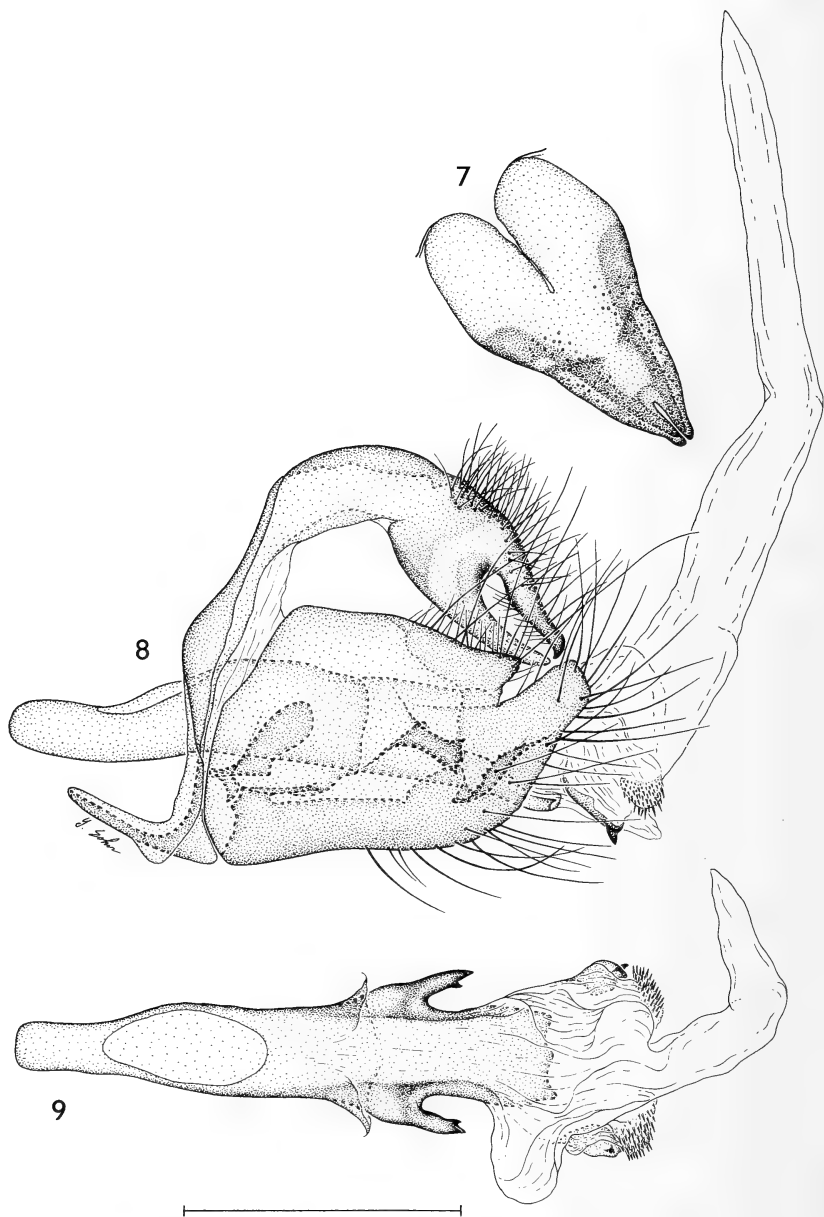
In *logan* group females (*flavens* not seen), the sclerotization in membrane between the ovipositor lobes is wide (Fig. 18) or, in *barbara*, absent (Figs. 22, 23); the lamella postvaginalis, moderately long; the ventral lip of the ostium bursae, relatively simple; and the ductus bursae, long (see Figs. 18, 19, 22, 23 for all the above characters).

Although well differentiated from one another, these species are more or less allopatric: *A. logan* occurs from extreme southcentral Canada, through most of the eastern and central United States, to extreme northeastern Mexico; *A. mazai*, from extreme southern Texas (Laredo [Freeman 1969]) and northeastern Mexico, through El Salvador, to Costa Rica (Guanacaste); *A. barbara*, from Colombia, through Ecuador, Venezuela, and the Guianas, to Peru and Brazil (Amapá, Pará, Rondônia); and *A. flavens*, in northern Argentina (Tucumán, Salta). This far-flung quartet forms two subgroups of two species each—a North American *logan* subgroup comprising *logan* and *mazai* and a South American *barbara* subgroup comprising *barbara* and *flavens*. *Anatrytone logan* and *A. mazai* are closer to each other, both morphologically and geographically, than are *A. barbara* and *A. flavens*. However, *logan* and *mazai* are not subspecies, as claimed by Scott (1986) and echoed by Opler and Malikul (1992). Indeed, though virtually allopatric, they are too different from each other even to be grouped in a superspecies.

In *A. logan* and *A. mazai*, the dorsodistal extension of the valva, viewed from the side, is dorsally broad (Fig. 5); the flexible "scouring-pad" cornuti are large and long and well sclerotized (Figs. 5, 6); the straight rigid cornuti have at least two to as many as five points (Figs. 5, 6); and the caudal prolongation of the aedeagal floor is blunt at its distal end (Fig. 6).

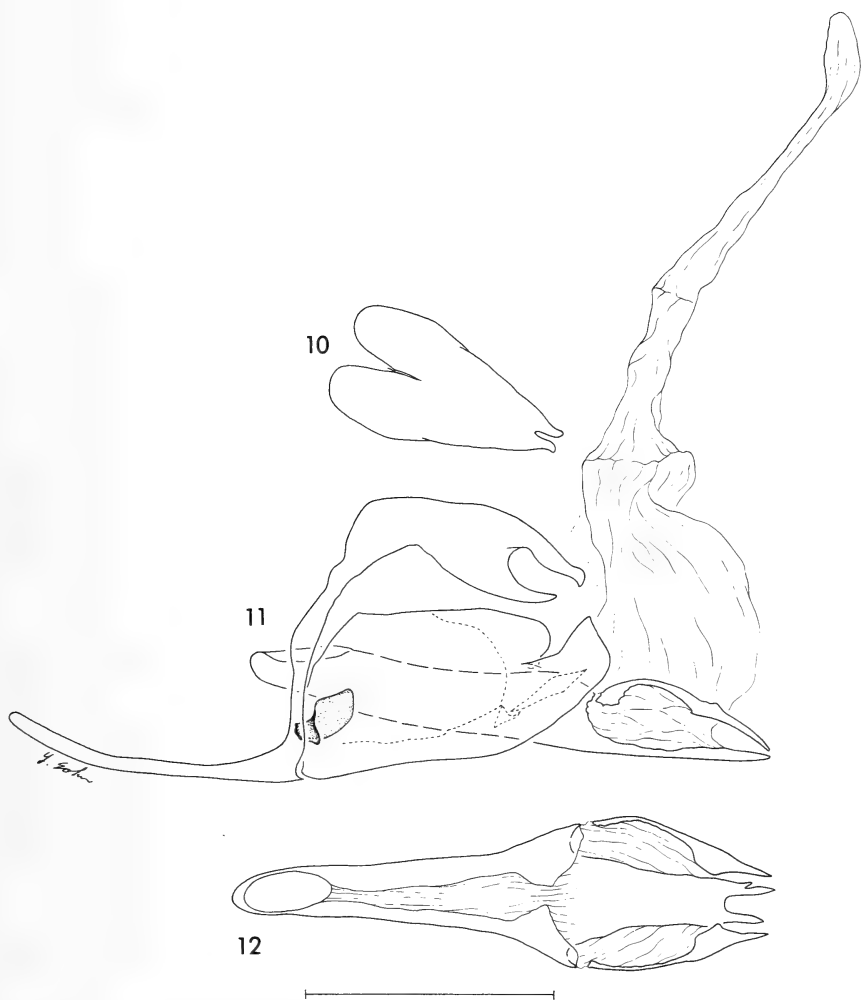
This prolongation is greater in *A. mazai* than it is in *A. logan*; the rigid cornuti of *mazai* are more than twice as long as those of *logan*; and the thin, platelike protrusion from the inner side of the dorsodistal extension of the valva is much larger—and arises much higher—in *mazai* than in *logan*.

In *A. barbara* and *A. flavens*, the dorsodistal extension of the valva, viewed from the side, is dorsally narrow (Figs. 11, 14); flexible cornuti are lacking (Figs. 11, 14); the long, curved rigid cornuti have either a



FIGS. 7-9. Male genitalia of *Anatrityone potosiensis* from San Pedro Sula, HONDURAS, 17 July 1979, R. D. Lehman (X-2573) (USNM). Scale = 1.0 mm. 7, Tegumen, uncus, and gnathos in dorsal view. 8, Complete genitalia (minus right valva), with vesica everted, in left lateral view. 9, Aedeagus, with vesica everted, in dorsal view.

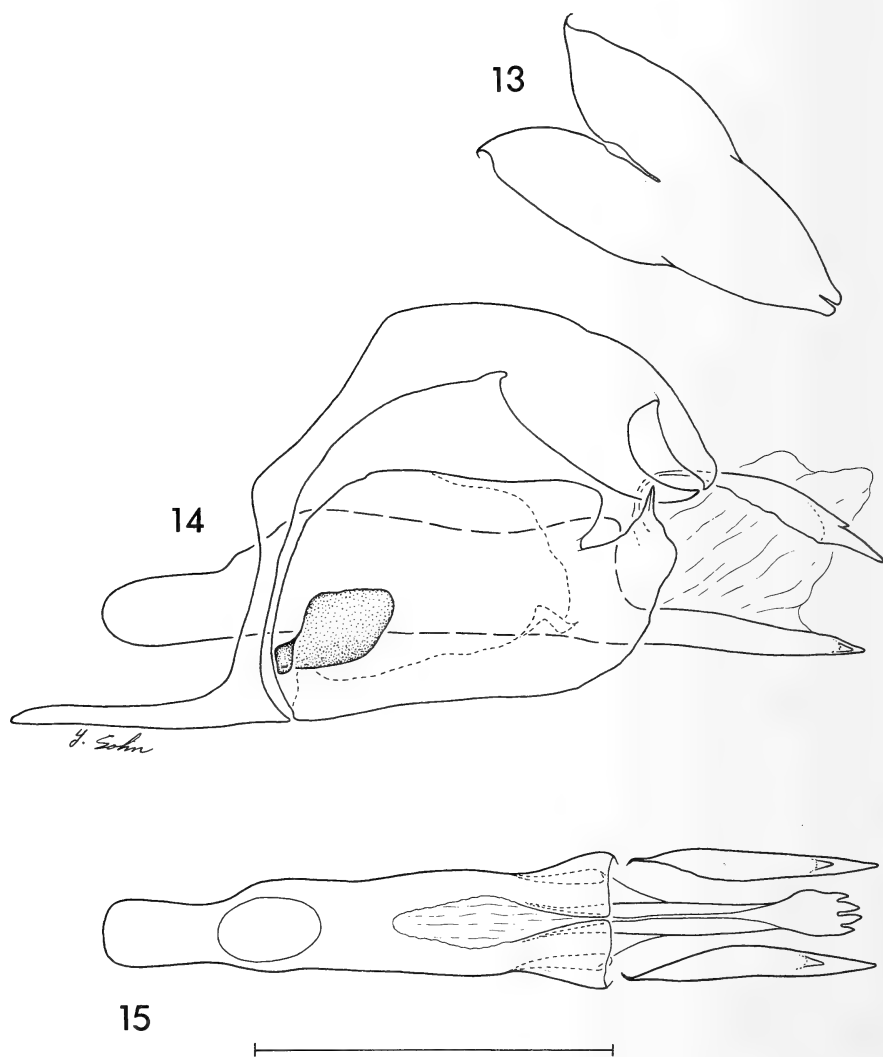




FIGS. 10–12. Male genitalia of *Anatriytone barbara* from 20 km SW Puerto Maldonado, 300 m, Madre de Dios, PERU, 25 October 1983, S. S. Nicolay (X-2585) (USNM). Scale = 1.0 mm. **10**, Tegumen and uncus in dorsal view. **11**, Complete genitalia (minus right valva), with vesica everted and juxta stippled, in left lateral view. **12**, Aedeagus (minus vesica) in dorsal view.

single (terminal) point (Figs. 11, 12) or such a point plus one small accessory point (Figs. 14, 15); and the caudal prolongation of the aedeagal floor is forked at its distal end (Figs. 12, 15).

The saccus is far shorter in *A. flavens* (Fig. 14) than it is in *A. barbara*, where it is nearly or quite as long as the valva (Fig. 11); the gnathos is



FIGS. 13-15. Male genitalia of *Anatrytone flavens* from Salta, ARGENTINA (X-3115) (Mielke collection). Scale = 1.0 mm. **13**, Tegumen and uncus in dorsal view. **14**, Complete genitalia (minus right valva), with vesica everted and juxta stippled, in left lateral view. **15**, Aedeagus (minus vesica) in dorsal view.

much shorter than the uncus in *A. barbara* (Fig. 11) though not in *A. flavens* (Fig. 14); the dorsodistal extension of the valva, viewed from the side, is dorsally extra narrow in *A. flavens* (Fig. 14); the caudal prolongation of the aedeagal floor is shallowly forked, with four tines at its distal end, in *A. flavens* (Fig. 15) but deeply and widely forked,

with two main tines (often equipped with one [Fig. 12] or occasionally two small secondary teeth), in *A. barbara* (Fig. 12); the sides of the caudal prolongation are distinctively rolled upward in *A. flavens* (Fig. 15) while the distal end of the aedeagus is more expanded in *A. barbara* (Fig. 12).

In both *A. logan* and *A. mazai*, as already noted, there is wide sclerotization in membrane between the ovipositor lobes (Figs. 18, 19); the ventral lip of the ostium bursae is not notably enhanced (Figs. 18, 19); the ductus bursae is not strongly flattened dorsoventrally, and its dorsal concavity is pronounced (Fig. 19); at most, the anterior quarter of the roof of the ductus bursae gives way to membranous corpus bursae (Fig. 19); and the tapering of the ductus bursae toward the ostium bursae looks prosaic (Fig. 18).

The dorsal concavity of the ductus bursae is simple throughout its length in *A. mazai* whereas a more or less anterior part of the dorsal concavity is divided longitudinally by a middorsal keel in *A. logan* (Figs. 18, 19); the ventral lip of the ostium bursae is unreinforced in *mazai* but lightly reinforced in *logan* (Figs. 18, 19).

In *A. barbara*, there is no sclerotization in membrane between the ovipositor lobes (Figs. 22, 23); the ventral lip of the ostium bursae is well reinforced and turned strongly downward and backward (Figs. 22, 23); the ductus bursae is quite flattened dorsoventrally, and its dorsal concavity is slight (Fig. 23); at least the anterior half of the roof of the ductus bursae gives way to membranous corpus bursae (Figs. 22, 23); and the ductus bursae tapers toward the ostium bursae with style (Fig. 22).

#### The *mella* Group

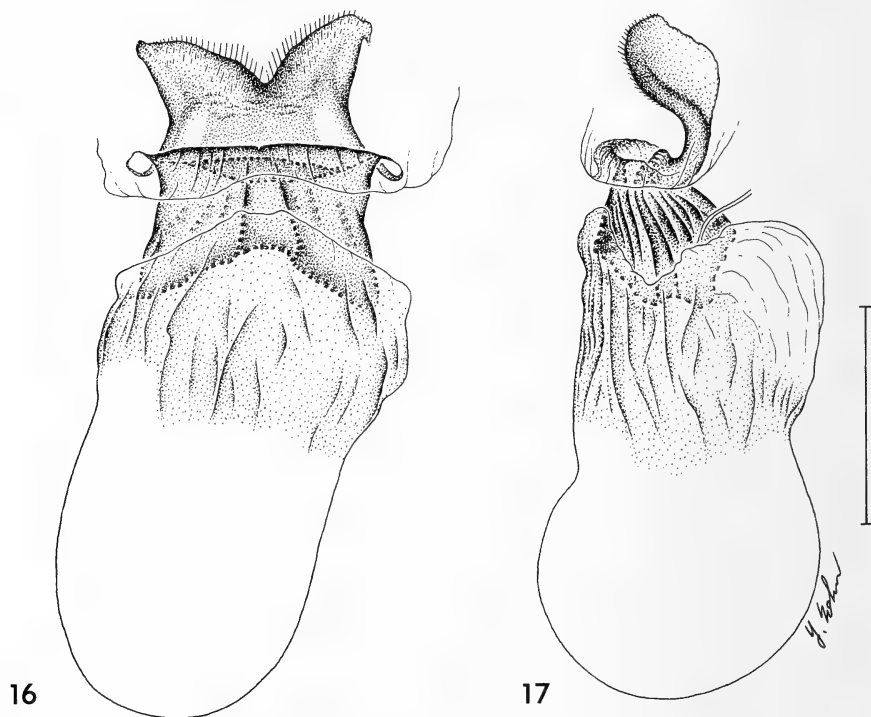
(Figs. 7-9, 20, 21, 24-27, 83-86)

*Anatrytone potosiensis* is the northernmost member of a compact, four-species group extending from Mexico to Argentina.

In males of the *mella* group, the saccus is short (Figs. 8, 27); conspicuous, paired titillators project from the sides of the aedeagus about where the caudal prolongation of the aedeagal floor begins (Figs. 8, 9, 24-27); the rigid cornuti are short (Figs. 8, 9, 24, 25) or lengthened by a peculiar base (Fig. 26); and the valvae are usually medium to extra high (Figs. 8, 27).

In *mella* group females, the sclerotization in membrane between the ovipositor lobes is narrow; the lamella postvaginalis, extra long; the ventral lip of the ostium bursae, well arched caudally and heavily sclerotized; and the ductus bursae, short (see Figs. 20, 21 for all the above characters).

Records of these closely related species indicate some sympatry with no breakdown in genitalic differences: *Anatrytone potosiensis* occurs



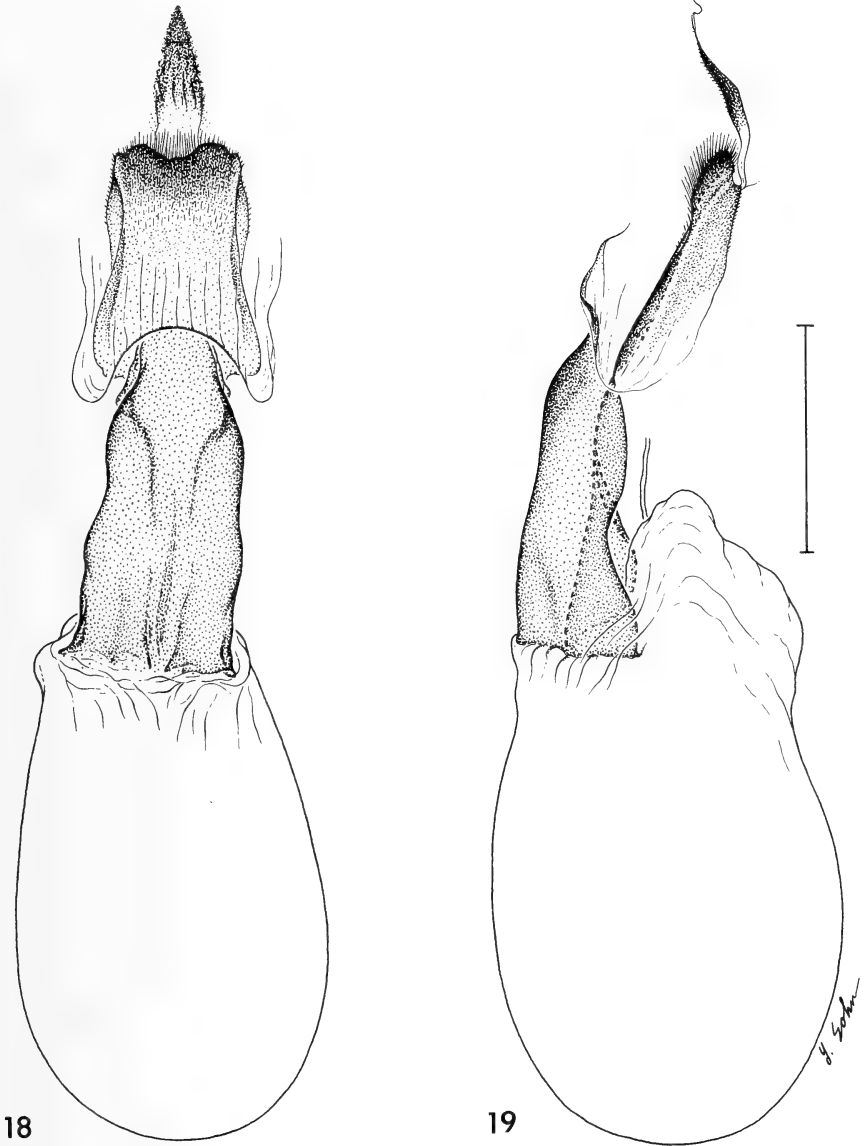
FIGS. 16, 17. Female genitalia of *Atrytone arogos* from Sioux City, Woodbury County, Iowa, USA, 26 June 1938, A. W. Lindsey (X-2745) (USNM). Scale = 1.0 mm. **16**, Sterigma and bursa copulatrix in ventral view. **17**, The same, plus part of the ductus seminalis, in right lateral view.

from central Mexico, through Guatemala, to Honduras; *A. mella*, from southern Mexico, through Central America (Guatemala, Belize, Honduras, Costa Rica, Panama), to Colombia and Peru; *A. sarah* (described below) from southern Colombia, through Ecuador and Peru, to Bolivia; and *A. perfida* (Möschler), from Colombia, Venezuela, Trinidad, Guyana, and French Guiana, through Brazil, to eastern Peru, Paraguay, and northern Argentina.

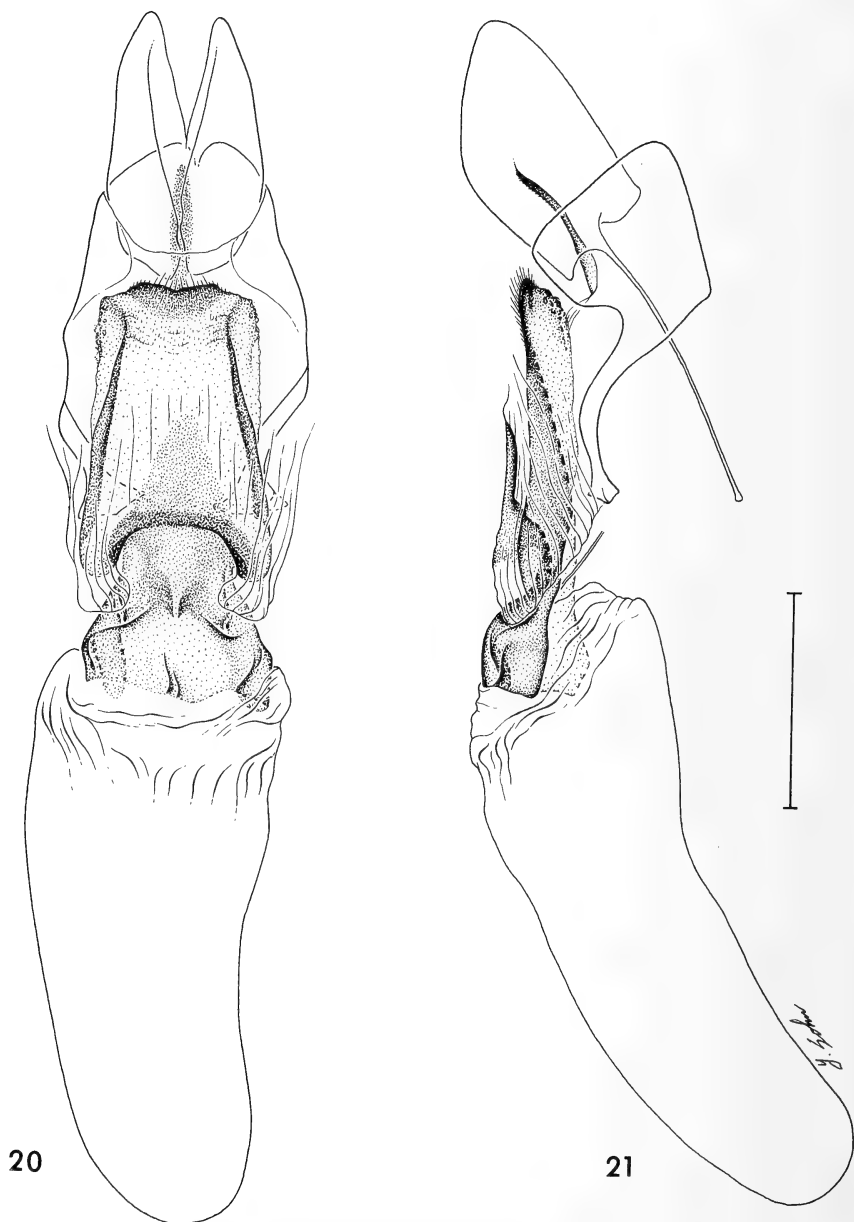
The following comparative description simultaneously characterizes all four species of the *mella* group; *sarah* is phylogenetically closest to *mella*.

***Anatrytone sarah*, new species**  
(Figs. 24, 83–86)

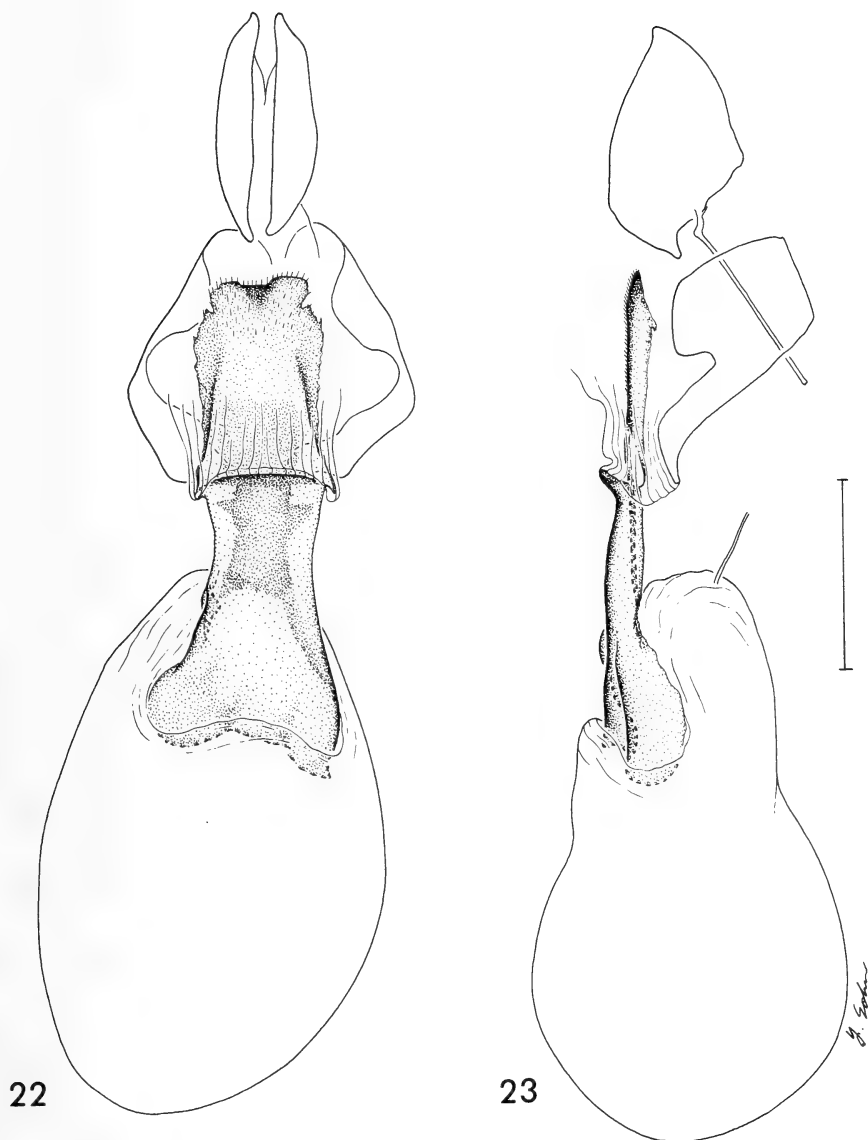
Most readily told by the aedeagus, especially the paired titillators which are longer and distally recurved in *sarah* (Fig. 24) and *mella* (Fig. 25) but shorter and divergent in



FIGS. 18, 19. Female genitalia of *Anatyrtone logan* from Austin, Travis County, Texas, USA, 14 May 1966, J. M. Burns (X-2627) (USNM). Scale = 1.0 mm. **18**, Sterigma and bursa copulatrix, plus linear sclerotization in membrane between ovipositor lobes, in ventral view. **19**, The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 20, 21. Female genitalia of *Anatrystone potosiensis* from Cotaxtla Exp. Sta., Cotaxtla, Veracruz, MEXICO, 31 July 1962 (X-2606) (USNM). Scale = 1.0 mm. **20**, Sterigma and bursa copulatrix, plus linear sclerotization in membrane between ovipositor lobes and an indication of the terminal abdominal tergites (including the ovipositor lobes), in ventral view. **21**, The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 22, 23. Female genitalia of *Anatrityone barbara* from Tambopata Reserve, Rio La Torre, 300 m, Madre de Dios, PERU, 2 November 1984, S. S. Nicolay (X-2829) (USNM). Scale = 1.0 mm. **22**, Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the ovipositor lobes) in ventral view. **23**, The same, plus part of the ductus seminalis, in right lateral view.

*potosiensis* (Figs. 8, 9) and *perfida* (Fig. 26). The titillators are shortest in *perfida*. In *sarah* (Fig. 24) they are abruptly constricted from a broad, knobby base and are bowed farther out than they are in *mella* (Fig. 25) whose basal taper is more even. They are also less flattened in *sarah* than in *mella* but lie more in a horizontal plane. In *sarah*, as in *mella* and most *perfida*, each titillator ends in a single point (Figs. 24–26), instead of in 2 to 4 (usually 3) points, as in *potosiensis* (Figs. 8, 9). (In one of the many males of *perfida* examined, the left titillator ends in 2 points.)

The caudal prolongation of the aedeagal floor is in *sarah* long, generally somewhat narrower than in other members of the *mella* group, continuously tapered from front to back, and distally truncate (Fig. 24); it is also truncate in *potosiensis* but relatively short and broad (Fig. 9). Though long, it is distally rounded in *mella* (Fig. 25) and rounded (Fig. 26) to somewhat truncate in *perfida*—and usually centrally notched in *perfida* (Fig. 26) but not in *mella* (Fig. 25). A lateral view shows it dipping downward sharply in *sarah*, less so in *perfida*, still less in *mella*, and little or not at all (Fig. 8) in *potosiensis*. Despite plenty of individual variation, these characters of the aedeagal floor are good.

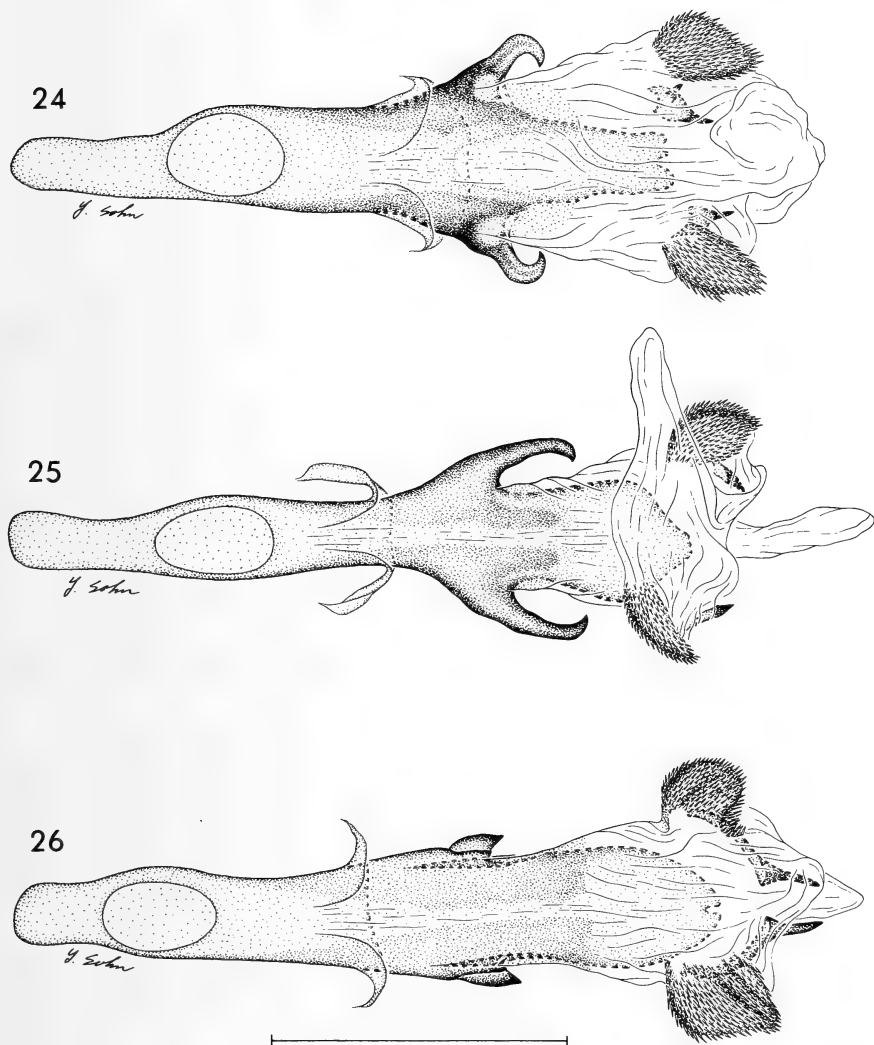
Development of both kinds of cornuti, taken together, is intermediate in *sarah*, greatest in *perfida*, least in *mella* and *potosiensis* (in different ways). The paired flexible cornuti ("scouring pads") are large and well sclerotized in *perfida* (Fig. 26), middle-sized and well sclerotized in *sarah* and *mella* (Figs. 24, 25), and small and lightly sclerotized in *potosiensis* (Figs. 8, 9)—to the extent that in one individual they virtually vanish. The paired rigid cornuti are largest in *perfida*, where each has an extra-long base—more or less arcuate in dorsal (Fig. 26) or ventral view—and a long point (which becomes dual on the left side in one of the many *perfida* examined). The rigid cornuti are middle-sized in *sarah*, where each has a respectable base and one or sometimes two usually longish points (the two-point condition can affect the left or the right [Fig. 24] cornutus). The rigid cornuti are also middle-sized in *potosiensis*, where each has a base at least as large as that of *sarah* but usually a shorter point (Fig. 9). They are smallest in *mella*, where they either have smallish to (more often) small, narrow bases and longish to (more often) short points (Fig. 25), or else are drastically reduced to a sliver (such vestigial cornuti can be on the left, on the right, or on both sides).

In ventral view the ventral lip of the ostium bursae forms a caudally directed arch, which is sharper in *sarah* and *mella* than in *potosiensis* (Fig. 20) and *perfida*. Although in all four species this lip curves downward (ventrad), it also curves conspicuously forward along both sides in *sarah* and *mella* but not in *potosiensis* (Figs. 20, 21) and *perfida*. Anterior to the lip region the ductus bursae is more or less lightly and incompletely sclerotized in *mella*, three-quarters to fully sclerotized in *sarah*, and fully sclerotized in *potosiensis* (Figs. 20, 21) and *perfida*. The arch of the ventral lip does not extend as far back in *sarah*, *mella*, and *potosiensis* as it does in *perfida*.

*Anatrytone sarah* is similar in size to other species of *Anatrytone* (except *barbara* and especially *flavens*, which are small), with the usual sex difference (females larger than males): 9 ♂♂ average 15.5 mm (range 14.9–16.1 mm) in forewing length; 2 ♀♀, 16.5 mm (range 16.4–16.6 mm).

The members of the *mella* group are similar (and, of course, individually variable) in superficial appearance—females so much that I cannot distinguish those of *sarah* (Figs. 85, 86) from those of *mella*, *perfida*, and *potosiensis* (on an average, however, females of *perfida* have the dorsal light areas a little more extensive and the yellow of the broad, ventral light areas brighter and clearer, less darkened with rust). Males of *sarah* (Figs. 83, 84) tend to be more distinctive because of the size and darkness of an irregular dark band in the dorsal forewing running obliquely from the base of the wing mainly through the upper part of the proximal half of space 1b, the proximal end of space 2, the length of the cell, and space 5, or spaces 4 and 5, to the wide dark border along the outer margin. This oblique dark band is variably, and usually less well, expressed in *mella* and especially *perfida* (some *mella* come close) and is completely missing from *potosiensis*. On the dorsal hindwing, males of *sarah* send a narrow, yellow orange ray along vein 1b to the outer margin (Fig. 83). Altogether, males of *sarah* approach the unusual, dorsal look of males of *barbara* of the *logan* group, except that other wing veins in *sarah* are still dark where they cross light areas (Fig. 83).





FIGS. 24–26. Aedeagi, with vesicae everted, in dorsal view, belonging to three species of *Anatrytone* in the *mella* group (compare also Fig. 9). Scale = 1.0 mm. **24**, *Anatrytone sarah* (holotype) from Limoncocha, 240 m, Napo, ECUADOR, 24–27 June 1980, C. V. Covell Jr. (H739) (USNM). **25**, *Anatrytone mella* from Macaracas, Los Santos, PANAMA, 22 December 1984, G. Small (X-2581) (USNM). **26**, *Anatrytone perfida* from Sapucay, PARAGUAY, W. T. Foster (X-2575) (USNM).

**Holotype.** ♂; ECUADOR, Napo (province), Limoncocha, 240 m, 24–27 June 1980, C. V. Covell Jr.; S. S. Nicolay genitalia dissection H739; USNM.

**Paratypes.** n = 8 ♂ 2 ♀. BOLIVIA, Santa Cruz (department), Las Juntas, 250 m, J. Steinbach: November 1913, 1 ♂, J. M. Burns genitalia dissection X-2836, CMNH; December 1913, 1 ♀, X-2843, CMNH. COLOMBIA, Amazonas (commissary), Leticia, 20 April 1946,

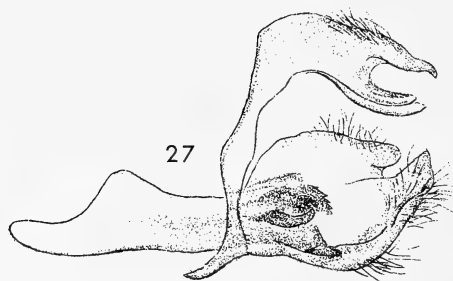


FIG. 27. Godman's figure of the male genitalia of *Anatrityone mella*; complete genitalia (minus left valva and juxta) in left lateral view. Note that, with the left valva removed, Godman's figure shows the inner surface of the right valva, whereas my figures show the outer surface of the left valva.

L. Richter, 1 ♂, E. L. Bell genitalia dissection G1911, AMNH; Puerto Asis, Rio Putumayo, 1 February 1969, S. S. Nicolay, 1 ♂, H484, USNM. ECUADOR, Napo (province): Archidona, 800 m, 13 October 1986, S. S. Nicolay, 1 ♂, H970, USNM; Coca, 350 m, 12 May 1975, Lefebvre, 1 ♂, X-3466, collection of O. H. H. Mielke; Pastaza (province), Puyo-Napo Road, km 25, 1100 m, 11 November 1988, D. H. Ahrenholz, 1 ♂, X-3204, collection of S. S. Nicolay. PERU, Loreto (department), 40 km NE Iquitos, 14–20 January 1991, J. Glassberg, 1 ♂, X-3175, USNM; Madre de Dios (department): Puerto Maldonado, 290 m, 14 October 1983, S. S. Nicolay, 1 ♀, X-2607, USNM; Boca Rio La Torre [=Tambopata Reserve], 300 m, 23 November 1983, G. Lamas, 1 ♂, X-2846, MUSM.

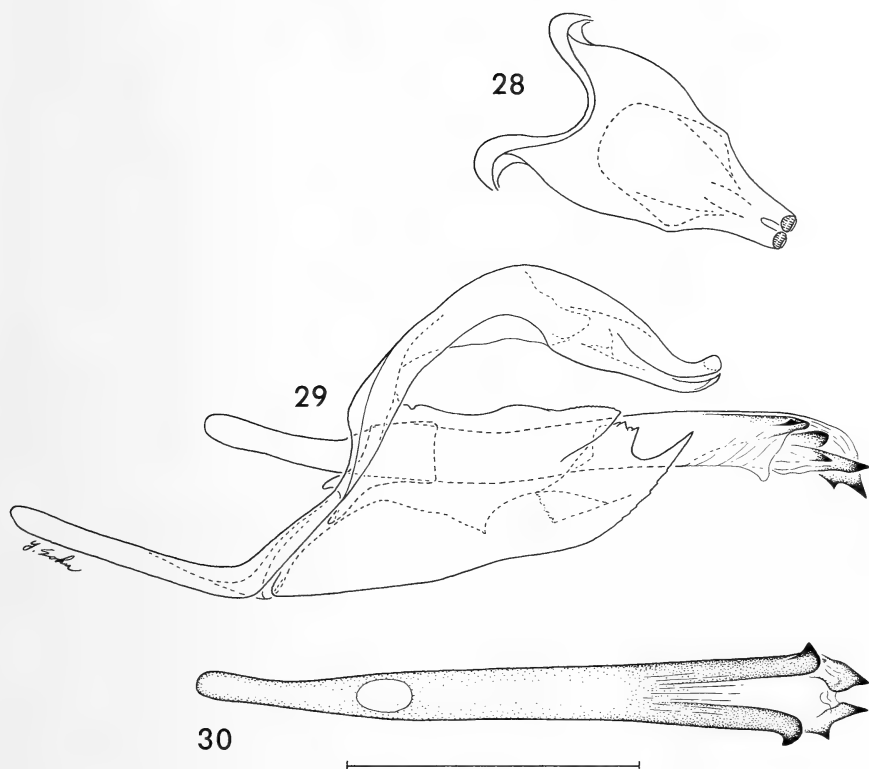
**Etymology.** The specific name *sarah*, which hails to and from my wife, is a noun in apposition to the generic name *Anatrityone*.

#### A TWIST OF NOMENCLATURE AND A DASH OF WALLENGRENIA (Figs. 27–30)

Besides the one of *sarah*, I have examined the types (also male) of *perfida* Möschler (1878) (ZMHB), *gladolis* Dyar (1914) (USNM), *flavens* Hayward (1940) (IML), *potosiensis* Freeman (1969) (AMNH), and *mazai* Freeman (1969) (AMNH).

When Dyar (1914) described *gladolis* he designated "Cotypes, one male, three females." I have studied all four specimens, which are similarly labelled and conspecific, and have chosen the lone male as lectotype. It bears the following tags, most of which are printed: [1] Georgetown/Br. Guiana, [2] BredSpecimen, [3] HWBMoore/Coll, [4, handwritten] Larva on blades/of sugar cane, [5, red] Type No./18115/U.S.N.M., [6, handwritten] Atrytone/gladolis/type Dyar, [7] GENITALIA NO./X-2831/J.M.Burns 1990. Although Dyar noted that *gladolis* is "nearest to *A. mella*," his original description (confined to the appearance and spread of the wings) is too brief and superficial to distinguish *gladolis* from *mella*—or from a good many other hesperiines, either. It turns out that *gladolis* Dyar (1914) is a (new) synonym of *perfida* Möschler (1878).

The original figure of the male genitalia of *A. mella* (Godman 1900:



FIGS. 28-30. Male genitalia of holotype of *Hesperia clavus* Erichson from British Guiana (X-2933) (ZMHB), which is a species of *Wallengrenia* similar to, or the same as, *W. otho*. Scale = 1.0 mm. **28**, Tegumen, uncus, and the very tip of the gnathos in dorsal view. **29**, Complete genitalia (minus right valva) in left lateral view. **30**, Aedeagus in dorsal view.

pl. 94, fig. 16 [reprinted in this paper as Fig. 27]) shows the short saccus characteristic of the *mella* group; the long, recurved titillator, evenly tapered at the base (less obvious in this lateral view), characteristic of *mella*; the "scouring-pad" cornuti characteristic of all species of *Anatrytone* except *barbara* and *flavens*; and a valva with the characteristic *Anatrytone* shape, but extra high. Valval height increases out of proportion to valval length in the *mella* group, especially in *mella*, *sarah*, and *potosiensis* (Fig. 8), and somewhat less consistently in *perfida*.

When Hayward (1948) described the new genus *Mellana*, he took as its type (and sole species) *Atrytone mella* Godman (1900), which he considered the same as *Atrytone gladolis* Dyar (1914). Since Hayward cited a specimen from northern Argentina (Misiones), his type species must really be *perfida* Möschler (1878) (= *gladolis* Dyar [1914]) instead

of *mella*; but that makes no difference. Both are congeneric with *Anatrytone logan* (Edwards), and *Anatrytone* Dyar (1905) has priority over *Mellana* Hayward (1948).

Evans (1955:354, 355) muddled his much expanded treatment of Hayward's (1948, 1950b) monotypic *Mellana* by calling *mella* Godman (1900) a synonym of *clavus* Erichson (1848)—which thus, in Evans's eyes, became the type of *Mellana*—and by listing *gladolis* Dyar (1914), *barbara* Williams & Bell (1931), and *flavens* Hayward (1940) as additional synonyms of *clavus*. I have shown that *gladolis* is a synonym of *perfida*, which is a species separate from *mella* but close to it, that *barbara* and *flavens* are very distinct from both of them and rather different from each other, and that all four go in *Anatrytone*. Having borrowed (from ZMHB) the holotype of *Hesperia clavus* Erichson (1848)—a male—and examined its genitalia (Figs. 28–30), I can flatly state that it is a species of *Wallengrenia*!

*Wallengrenia clavus* (Erichson), new combination, is what Evans (1955 plus associated "Addenda and Corrigenda") called *W. otho curassavica* (Snellen). The name *clavus*, being older, supplants the name *curassavica*. The biologic entity *clavus* closely resembles *otho* Smith (1797), differing chiefly in the direction of the terminal tooth on the right (the longer) distal division of the aedeagus: that tooth points up and to the right in *clavus*, up and to the rear in *otho* (compare Figs. 29, 30 with figs. 11–14, 19–22 in Burns 1985). The type of *clavus* comes from Guyana. In a crude transect—12 more tails of *Wallengrenia* males from Mexico to Brazil—the right aedeagal tooth points up and to the right in the six males from Panama, Colombia, Guyana, and French Guiana, but not in those from farther north or south. Some features of the pair of terminal, dependent, two-toothed cornuti (dubbed "flags" in Burns 1985) also appear to vary geographically. Whether *clavus* is a synonym of *otho*, a subspecies of *otho*, or a separate species is a problem beyond the scope of this paper.

After blindly synonymizing *barbara* with three other species of *Anatrytone* and *Wallengrenia clavus*, Evans (1955:359) went on to describe new species *Mellana villa*, which Mielke (1973) pegged as a synonym of *M. barbara* (Williams & Bell)! Mielke also observed that *M. barbara* was not synonymous with *M. clavus* (Erichson).

Note that *Atrytone*, *Anatrytone*, and *Quasimellana* (the new genus, described below, for most of what was in *Mellana*) all lack a stigma on the forewing of the male whereas *Wallengrenia* bears a bold stigma.

#### Summary of *Atrytone* and *Anatrytone*

The following capsule of my treatment of *Atrytone* and *Anatrytone* gives the number of male and female genitalia examined at each level—

140 dissections in all. I list neither subspecies nor synonyms of *Atrytone arogos* and *Anatrytone logan* because I did not investigate these familiar nearctic skippers at that low level. Such information is readily available in checklists (Miller & Brown 1981, 1983). Repeating it here would amount to empty endorsement of what may be faulty or undocumented opinion—the kind of deed that has left much of our taxonomy a shambles.

*Atrytone* Scudder, 1872, 10 ♂ 15 ♀, n = 25

*arogos* (Boisduval & Leconte, [1834]), 10 ♂ 15 ♀

*Anatrytone* Dyar, 1905, 82 ♂ 33 ♀, n = 115

= *Mellana* Hayward, 1948, new synonym

the *logan* group, 31 ♂ 14 ♀

the *logan* subgroup, 14 ♂ 10 ♀

*logan* (Edwards, 1863), 8 ♂ 8 ♀

*mazai* (Freeman, 1969), new combination, 6 ♂ 2 ♀

the *barbara* subgroup, 17 ♂ 4 ♀

*barbara* (Williams & Bell, 1931), new combination, 15 ♂ 4 ♀

= *villa* (Evans, 1955)

*flavens* (Hayward, 1940), new combination, 2 ♂

the *mella* group, 51 ♂ 19 ♀

*mella* (Godman, 1900), new combination, 14 ♂ 11 ♀

*sarah* Burns, new species, 9 ♂ 2 ♀

*potosiensis* (Freeman, 1969), new combination, 6 ♂ 1 ♀

*perfidia* (Möschler, 1878), new combination, 22 ♂ 5 ♀

= *gladolis* (Dyar, 1914), new synonym

#### Major Generic Characters in the Smallest Genitalic Structures

What remains after subtracting species of *Anatrytone* (and *Wallengrenia clavus*) from *Mellana* as treated by Evans (1955) is an unnamed and difficult neotropical genus at least thrice the size of *Anatrytone* and far more diverse. Ranging from the extreme southern United States (southern Texas; perhaps also southern Arizona—see Bailowitz & Brock 1991) to Peru, Bolivia, Paraguay, and northern Argentina, new genus *Quasimellana* (described below) is broadly sympatric with *Anatrytone*. Both occur from sea level to moderate elevations. Despite some similarities in superficial appearance, which cause confusion, *Quasimellana* and *Anatrytone* are not closely related.

We have seen that the genitalia of *Anatrytone* are basically conservative (in both sexes) and hence invaluable for defining that genus. In gross view, those of *Quasimellana* are signally variable, especially in males (females of a quarter of the species are not yet known): the large middorsal structures (tegumen/uncus plus underlying gnathos) and the

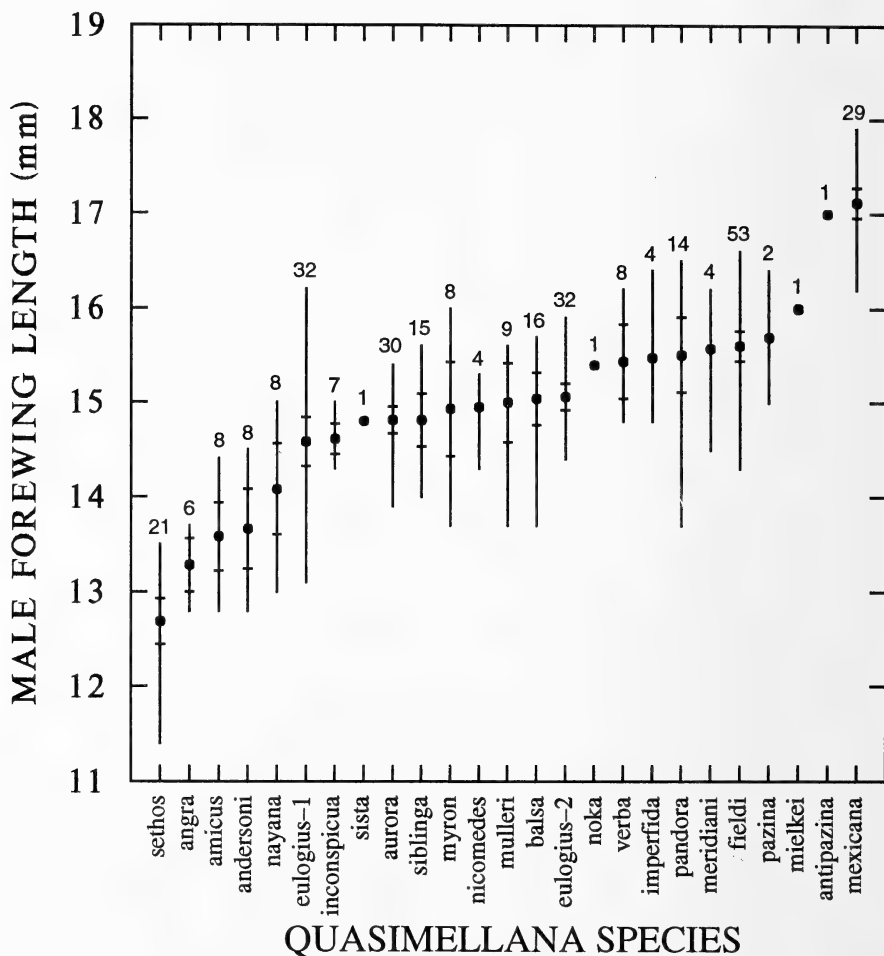
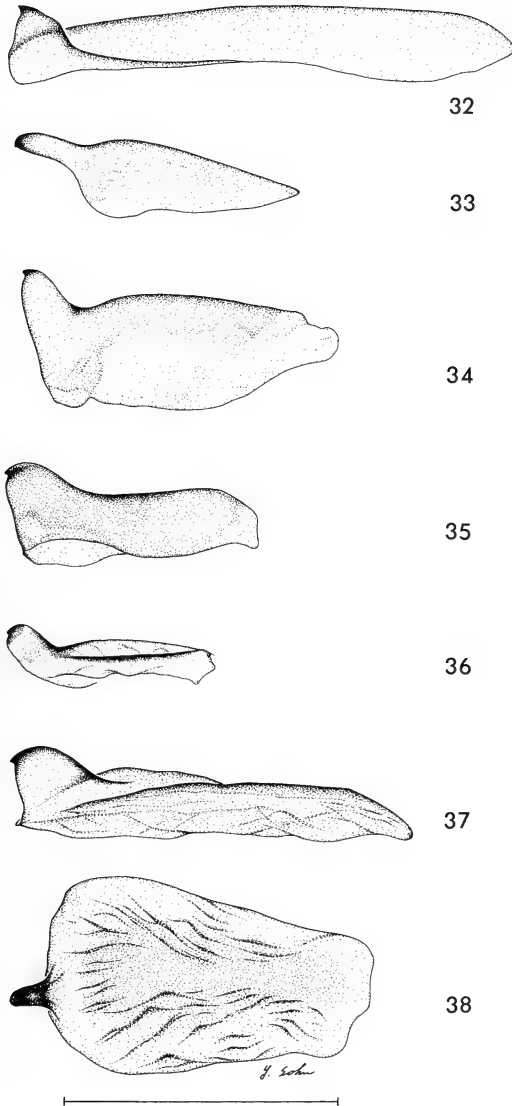


FIG. 31. Size (male forewing length) in species of *Quasimellana* from smallest to largest. Vertical lines show ranges; dots, means (or single observations); crossbars, plus and minus twice the standard error of the mean (when the sample size exceeds five). Sample sizes appear above the range lines. There are two geographic subsamples of the widespread and relatively common *Q. eulogius*: *eulogius*-1 from Mexico and *eulogius*-2 from Honduras, Nicaragua, Costa Rica, and Panama.

large, paired lateral structures (valvae) assume too many forms to permit generalizing across the whole genus. But what do characterize *Quasimellana* are two relatively small and obscure genitalic structures currently lacking the "respect and attention" (Burns 1987:184) they deserve: the cornutus and the juxta.

The shape of the cornutus alone is diagnostic. Though it does vary within—and more perceptibly between—species, the variation is so



FIGS. 32–38. Cornuti of six species of *Quasimellana* showing variations on an essential theme. Scale = 0.5 mm. **32**, *Q. eulogius* from Ciudad de Valles, San Luis Potosí, MEXICO, 13 October 1976, E. C. Knudson (X-2587) (USNM). **33**, *Q. mexicana* (X-2586) shown fully in Figs. 40, 41 (qv for specimen data). **34**, *Q. fieldi* (X-2571) whose juxta appears in Fig. 39 (qv for specimen data). **35**, *Q. nicomedes* from Cacatu, Antonina, 20 m, Paraná, BRAZIL, 25 April 1973, Mielke (X-2366) (MacNeill collection). **36**, *Q. sethos* from Paraíso, Canal Zone, PANAMA, 27 April 1982, S. S. Nicolay (X-2595) (USNM). **37**, **38**, *Q. mulleri* (paratype) from Guerrero, MEXICO, August, R. Müller (X-2669) (AMNH).

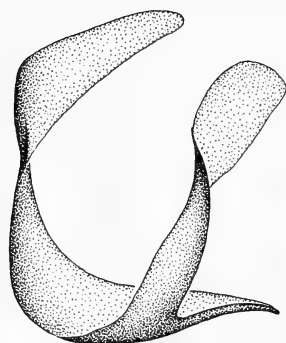
TABLE 1. Number of antennal nudum segments in species of *Quasimellana*.

Species groups and species	Mean	Number of nudum segments						n
		11	12	13	14	15	16	
<i>eulogius</i> group								
<i>mexicana</i>	13.3			19	8			27
<i>eulogius</i>	13.4	1	6	56	39	5	1	108
<i>siblinga</i>	14.3			1	9	6		16
<i>balsa</i>	13.4		1	9	6	1		17
<i>mulleri</i>	12.9		1	9				10
<i>sethos</i> group								
<i>aurora</i>	13.7			9	12	2		23
<i>nayana</i>	14.4			1	3	4		8
<i>pazina</i>						2		2
<i>antipazina</i>						1		1
<i>sista</i>						1		1
<i>andersoni</i>	14.8				1	4		5
<i>sethos</i>	14.0			4	16	1	1	22
<i>myron</i>	12.9		1	10				11
<i>verba</i>	13.5			4	4			8
<i>inconspicua</i>	13.4		1	3	4			8
<i>angra</i>	14.2			2	4	4		10
<i>nicomedes</i> group								
<i>amicus</i>	13.2			8	2			10
<i>fieldi</i>	14.2		1	3	42	17	1	64
<i>nicomedes</i>	15.2				1	3	2	6
<i>imperfida</i>	14.8				1	4		5
<i>mielkei</i>							2	2
<i>meridiani</i>	15.5					2	2	4
<i>pandora</i>	15.5					6	5	11

constrained that a single, simple generic theme stands out (Figs. 32–38). Since the sclerotized cornutus sits in the membranous vesica which, except during copulation, rests collapsed and folded within the sclerotized aedeagus, the vesica must be everted for a really good look at the cornutus (Figs. 41, 43, 45, 47, 49, 50, 52, 53, 55, 57, 59, 60, 62, 65, 67).

The shape of the juxta (Fig. 39) is likewise diagnostic; but so, too, is its location. An apparent support for the aedeagus, the juxta lies ventral and lateral to it at about the level of the anterior ends of the paired valvae and the adjacent vinculum to which they articulate. Typically, in a lateral view of male genitalia, the juxta is largely to entirely hidden behind the vinculum and the front end of a valva. That is where it is in *Atrytone* (Fig. 2), *Anatrytone* (Figs. 5, 8, 11, 14), and *Wallengrenia* (Fig. 29); in many other genera thought to be related to these (i.e., in the *Hesperia* subgroup of the M or *Hesperia* group of Evans 1955), such as *Hesperia* itself (Burns 1987, fig. 2), *Atalopedes* (Burns 1989,





39

FIG. 39. Juxta, in left anterodorsolateral view, of *Quasimellana fieldi* from 15.4 mi (24.8 km) S Ciudad de Valles, San Luis Potosí, MEXICO, 22 August 1967, G. F. Hevel (X-2571) (USNM).

figs. 25, 27, 29, 31, 33), *Polites* (Burns 1994, fig. 14), *Poanes* (Burns 1992, figs. 2, 5), *Paratrytone* (Burns 1992, fig. 20), and the like; and in a great many other skippers, as well. However, in *Quasimellana* the juxta is so far forward that most of it shows in lateral view (Figs. 41, 43, 45, 47, 52, 55, 57, 59, 62, 65, 67).

Since the location of the juxta is crucial, I regret to say that it can rarely be determined from published figures of skipper genitalia. In most of them, the juxta does not even appear (see Fig. 27, which exemplifies the many genitalic figures in Godman & Salvin 1879–1901). When it does, it almost always accompanies the aedeagus in an exploded view of the genitalia, displaced from its true position and from its proper relation to other parts. The common practice of dissociating major structures such as the valvae or the aedeagus when dissecting male genitalia, often destroys the juxta. Evans's mode of quick dissection and dissociation routinely did away with it (Figs. 49, 50, 53, 60).

### ***Quasimellana*, new genus** (Figs. 31–82, 87–112)

**Size.** Male forewing length ranges from 11.4 to 17.9 mm; but, in most species, mean male wing length falls between 14 and 16 mm (Fig. 31). The relatively few females available always average larger than conspecific males.

**Nudum.** Ranging from 11 to 16 segments, the nudum usually numbers 13 to 15 segments (though often to 16 segments in the *nicomedes* group), evenly split between the body of the club and the apiculus (Table 1).

**Stigma.** Males do not have a stigma.

**Male genitalia.** The sole (or only sizable) rigid cornutus consists of a simple body with a head-and-neck that ends in a tiny hook (Figs. 32–38, 41, 43, 45, 47, 49, 50, 52, 53, 55, 57, 59, 60, 62, 65, 67). The entire structure is well sclerotized and conspicuous.

The juxta resembles a **U** whose paired, lateral, upright arms twist once into more or

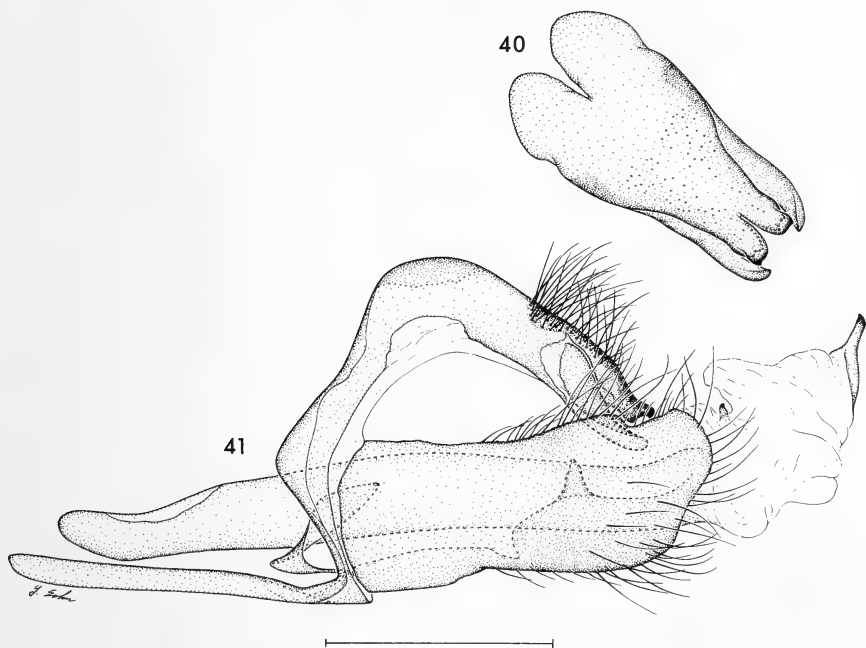
less expanded and posteriorly trending upper ends while the base of the **U** gives off a long, midventral, posteriorly tapering triangle (Fig. 39). The juxta sits unusually far forward, largely exposed in lateral view (Figs. 41, 43, 45, 47, 52, 55, 57, 59, 62, 65, 67).

**Female genitalia.** The posterior margin of the lamella postvaginalis gives rise mid-ventrally to a single, posteriorly directed, bristly projection (Figs. 68–82). This central projection may be only slightly developed (Fig. 76) or remarkably wide (Fig. 74), but usually it is narrow and long (Figs. 68–73, 75, 77, 81, 82) to very long (Figs. 78–80).

**Type species.** *Atrytone mexicana* Bell (1942b:461, fig. 5). Figs. 33, 40, 41 (male genitalia); 68, 69 (female genitalia); 87, 88 (adult male); and 89, 90 (adult female).

Individually rather plain, the male genitalia are so interspecifically variable that they seem elaborate in *Quasimellana* as a whole. The tegumen/uncus varies from narrow to wide. The distal end of the uncus varies from about as thick as, to much thicker than, the distal end of the gnathos; from decidedly longer to decidedly shorter than the gnathos; from close above the gnathos to far above it; from undivided to well divided; the uncal divisions, from closely parallel to widely divergent—and then, in one case, bent sharply upward, besides. The distal end of the valva may have zero, one, or two projections, each ranging from broadly rounded to sharply pointed and extending primarily dorsad or caudad (sometimes mediad, as well). The inner side of the valva may develop a triangular middle process, a more oblong dorsal process, both of these, or neither. The aedeagus is a simple tube (devoid of titillators and terminal teeth or prongs) about as long as the total intact genitalia (i.e., saccus plus valvae), but its vesica varies from long, narrow, and fingerlike to shorter and less regular, with protruding, armlike pouches; the diagnostic cornutus, situated near or at the distal end of the everted vesica, may or may not be accompanied by a tiny, secondary, apparently vestigial cornutus near the proximal end of the vesica. The diagnostic cornutus itself varies from short to long and from narrow to wide; in the shape, height, point of attachment, and angle of the head-and-neck on the body; and the body varies from convex to concave, as well as in certain minor decorations. The saccus is usually much shorter than the valva but may approach it or even exceed it in length. The juxta varies in just how far forward it sits, in the height of the twist in each arm, and in details of shape.

Each species account begins (after any synonymy) with two or three kinds of crucial information in condensed form: (1) mention of the holotype, its sex, and its location (abbreviated, for example, “HT♂-USNM”) whenever I have seen and studied that specimen and its genitalia; (2) the spatial distribution (based on material examined), arranged geographically by country (and, in the United States, Mexico, Brazil, and Argentina also by state, territory, or province), plus a few important additions from the literature; and (3) the numbers of males and females examined, followed (in parentheses) by the number of genitalia compared in each sex. Whenever I have studied the holotype

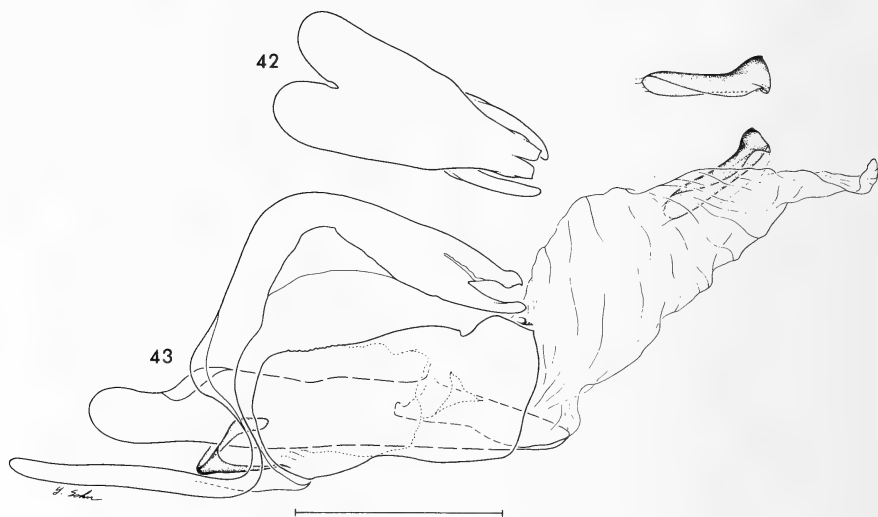


FIGS. 40, 41. Male genitalia of *Quasimellana mexicana* from San Luis Potosí, San Luis Potosí, MEXICO, 3 August 1941, A. H. Moeck (X-2586) (USNM). Scale = 1.0 mm. **40**, Tegumen, uncus, and gnathos in dorsal view. **41**, Complete genitalia (minus right valva), with vesica everted, in left lateral view.

of a synonym, hyphenated abbreviations as in (1) end the entry in the synonymy.

I have examined the genitalia of the types of two species (besides *Wallengrenia clavus*) put in *Mellana* by Evans (1955) but belonging neither in *Quasimellana* nor in *Anatrytone*: *gala* Godman (1900) (USNM), from Mexico, which Evans questioningly listed as a synonym of *monica* Plötz (1886), from southern Brazil (Santa Catarina); and *rivula* Mabilie (1891) (ZMHB), which Evans treated as a species with two subspecies—*rivula*, from northern Brazil (Amazonas), and *amicus* Bell (1942), from Ecuador (although *rivula* is not a species of *Quasimellana*, *amicus* is).

Though I amassed some 450 specimens in my study of *Quasimellana*, only 12 out of 24 species are represented by more than 10 specimens, but 7 of those are represented by more than 20; another 7 species are known from 6 or fewer specimens, and 3 of these (including 2 that Evans described back in 1955), from just 1. In light of these figures, the large (essentially neotropical) range of the genus, and the superficial similarities among various differentiates, additional species doubtless



FIGS. 42, 43. Male genitalia of paratype of *Quasimellana siblinga* from El Vado-San Sebastian, 5500–6500 ft (1675–1980 m), ca 16° 53' N, 96° 53' W, Oaxaca, MEXICO, 22 June 1992, J. Kemner (X-3592) (USNM). Scale = 1.0 mm. **42**, Tegumen, uncus, and gnathos in dorsal view. **43**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view (plus primary cornutus in profile).

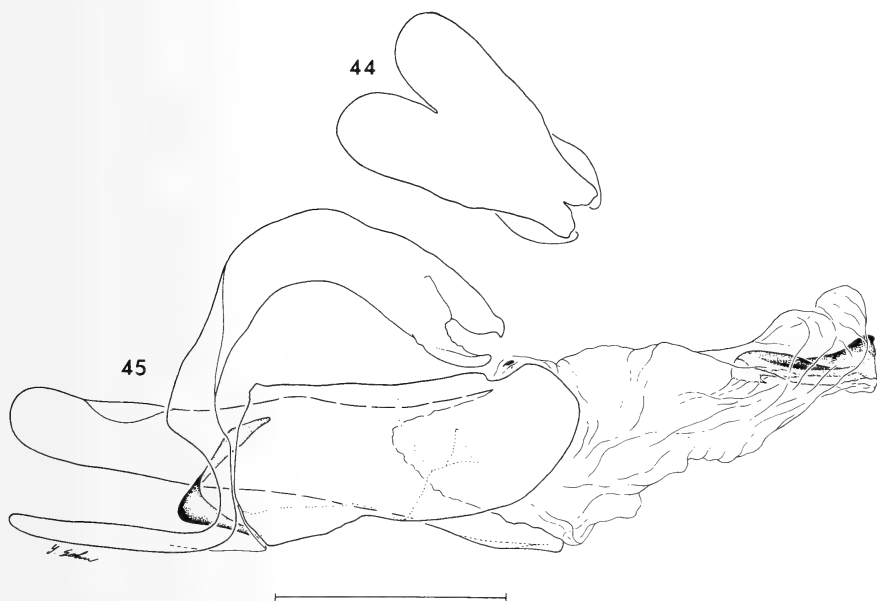
await discovery; and for most described species, knowledge of geographic distribution leaves much to be desired.

## THE SPECIES GROUPS AND SPECIES OF *QUASIMELLANA*

### The *eulogius* Group

(Figs. 31–33, 37, 38, 40–45, 68–73, 87–92)

**Male genitalia.** *Juxta*: The juxta is posterior in location (Figs. 41, 43, 45), as it is in *nayana*, *aurora*, and *andersoni* of the *sethos* group (Figs. 47, 55). The level of the twist in each lateral arm of the juxta is low (Figs. 41, 43, 45), as it is in the *sethos* group (Figs. 47, 52, 55, 57, 59). *Cornutus*: Except in *mexicana* (Figs. 33, 41), the head-and-neck of the cornutus is short, wide, and upright (Fig. 37) to backswept (Figs. 32, 43, 45). Its position on the body of the cornutus varies from central (Figs. 33, 41) to left of center (Fig. 38) to left (Figs. 32, 43, 45). The body of the cornutus is narrow except in *mulleri* (Figs. 37, 38). The tiny, secondary, vestigial cornutus is present (Figs. 41, 43, 45), except in two examined individuals of *mulleri* and one of *siblinga*, as it usually is in the *sethos* group (Figs. 47, 49, 52, 55, 57, 60). *Vesica*: The everted vesica is relatively short (Figs. 41, 43, 45). *Valva*: On its inner surface, the valva always has a middle process, which is relatively large and long (Figs. 41, 43, 45), but never the dorsal process that marks the *sethos* group (Figs. 49, 50, 52, 53, 55, 57, 59, 60). In lateral view the dorsodistal end of the valva is simple and more or less broadly rounded (Figs. 41, 43, 45), without prominent sharp points or projections. *Uncus*: The distal end of the uncus is deeply divided, with the resultant prongs more or less close together and parallel (Figs. 40, 42, 44). In lateral view, the distal end of the uncus is only a little thicker than the distal end of the gnathos



FIGS. 44, 45. Male genitalia of *Quasimellana balsa* from 23 mi (37 km) S Ixtapan de la Sal, Guerrero, MEXICO, 16 August 1981, J. A. Chemsak (X-2803) (UCB). Scale = 1.0 mm. **44**, Tegumen, uncus, and gnathos in dorsal view. **45**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

(Figs. 41, 43, 45), as it is in the *sethos* group (Figs. 47, 49, 52, 55, 57, 59) plus *amicus* of the *nicomedes* group.

**Female genitalia.** The anterior apophyses are long (Figs. 68, 69, 72, 73) except in *balsa* (Figs. 70, 71), where they are intermediate to short (the female of *siblinga* is unknown). The corpus bursae is relatively long and narrow (Figs. 68–73).

**General features.** Sexual dimorphism is strong (Figs. 87–90), except in *mulleri*. Males are always extensively yellowish-orange and blackish-brown dorsally, with dark veins. The species are medium to large in size (Fig. 31).

**Distribution.** Although the *eulogius* group (with 5 species) extends from the United States (south Texas) to Brazil and Paraguay, it is mainly North American.

*Quasimellana mexicana* (Bell, 1942b:461, fig. 5),  
new combination  
(Figs. 31, 33, 40, 41, 68, 69, 87–90)

HT♂-USNM. Mexico (San Luis Potosí, Veracruz, Nayarit, Guerrero, Oaxaca), Guatemala, Belize. 29 ♂ 8 ♀ (16 ♂ 4 ♀).

The largest species of *Quasimellana* (Fig. 31), *mexicana* has a narrow cornutus with a distinctive, long, narrow head-and-neck obliquely stretched far in front of the body (Figs. 33, 41). The saccus is relatively long for *Quasimellana* (even for *mexicana*, however, the saccus of the individual in Fig. 41 is unusually long). The sclerotized lateral lobes of the lamella postvaginalis (on either side of the midventral, posteriorly directed, bristly projection) do not extend as far caudad as they do in most species of *Quasimellana*, while the ductus bursae is unusually plain (compare Figs. 68, 69 with Figs. 70–82).

*Quasimellana eulogius* (Plötz, 1883:64), new combination  
(Figs. 31, 32, 72)

= *mellona* (Godman, 1900:493, pl. 94, figs. 17-19).

= *heberia* (Dyar, 1914:5), lectotype ♂ (J. M. Burns genitalia dissection X-2832) here designated from 3 cotypes (2 ♂ 1 ♀ bred from larvae on blades of sugarcane, Georgetown, British Guiana, H. W. B. Moore, type no. 18116) in USNM.

= *agnesae* (Bell, 1959:13, figs. 8, 21), new synonym, HT♂-AMNH.

= *oaxaca* (Freeman, 1979:10, figs. 20, 21, 29 [valva upside down]), new synonym, HT♂-AME.

United States (south Texas—Cameron and Hidalgo counties), Mexico (Nuevo León, San Luis Potosí, Sinaloa, Veracruz, Puebla, Guerrero, Oaxaca, Chiapas, Yucatán, Quintana Roo), Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Guyana, Brazil (Pará, Espírito Santo); Evans (1955) also records Bolivia and Paraguay. 80 ♂ 30 ♀ (49 ♂ 29 ♀).

For *Quasimellana eulogius* is unusually common and widespread—the seeming “weed species” of the genus. The large size and latitudinal and altitudinal diversity of my *eulogius* sample may explain why it showed the most individual variation (reflected, for example, in Fig. 31 and Table 1). But then again, it may include more than one species; and some of the above synonyms—particularly *heberia* and *agnesae*—may need resurrection.

Godman (1907) promptly sank his *mellona* Godman (1900) to *eulogius* Plötz (1883). In describing *agnesae* (from two males taken 6 and 9 December 1939 in Acapulco, Guerrero, Mexico), Bell (1959:13) called it “a small species of *Mellana*, with different genitalia from those of its nearest relatives.” I have examined the holotype and paratype and Bell’s slides of their genitalia, which look just like those of *eulogius*. Although the small size (forewing length 12.2 and 12.7 mm) and greater extent of yellow orange coloring do differ from ordinary *eulogius* (Fig. 31), I have measured an equally dwarf (12.6 mm) but normal looking *eulogius* male from Guatemala and have seen normal sized but equally yellow orange *eulogius* males from Sinaloa, Mexico, and Brownsville, Texas. At least for now, I conservatively view the specimens of *agnesae* as light runts of *eulogius*.

See *siblinga* for characterization of the male genitalia of *eulogius* (which are well shown in lateral view—including the extra long, narrow cornutus [Fig. 32]—in Godman 1900: pl. 94, fig. 19).

The female genitalia (Fig. 72) depart from those of other known *Quasimellana* females because the ductus bursae is extremely short, and its main sclerotization (in ventral view) is a narrow band around it; the midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is usually fairly long and narrow, without any laterally expanding sclerotization at its base; and the sclerotized lateral lobes that flank this projection are relatively narrow. (The female genitalia assigned to a paratype of *Mellana tecla* Steinhauser and to undetermined females of *Mellana* in figs. 82, 88, and 89 of Steinhauser 1974 all come from *eulogius*; even a delicate, female character state that I broadly ascribe to the *eulogius* group—long anterior apophyses—shows in these photographs.)

At present, I can cleanly pull the following species from a possible *eulogius* complex.

*Quasimellana siblinga*, new species  
(Figs. 31, 42, 43, 91, 92)

HT♂-USNM. Mexico (Sonora, Sinaloa, Oaxaca). 16 ♂ (9 ♂).

Superficially and genitally reminiscent of *eulogius* and *balsa*. Primary cornutus (Fig. 43) similarly linear and narrow, about as long as in *balsa* (Fig. 45)—therefore much shorter than in *eulogius* (Fig. 32)—but body of cornutus dorsally convex and without the longitudinal twist of both *eulogius* (Fig. 32) and *balsa* (Fig. 45). Secondary, vestigial cornutus (Fig. 43) smaller than in *eulogius* (completely gone in one individual). In lateral view, dorsodistal end of valva somewhat truncate dorsally (Fig. 43) and so less rounded than in *eulogius* and *balsa* (Fig. 45). Ventrodistal corner of valva (Fig. 43) not cut away

as in *eulogius*. Tegumen, uncus, and gnathos (as well as distal end of aedeagus) (Figs. 42, 43) much less massive than in *balsa* (Figs. 44, 45), and uncus prongs (Fig. 42) less widely notched than in *balsa* (Fig. 44)—all about as in *eulogius*; but each uncus prong proximally with a ventrolateral swelling (Figs. 42, 43)—not present in *eulogius*—large enough to show in dorsal view (Fig. 42). Gnathos slightly longer than uncus (Figs. 42, 43). Medium sized species, close to fellow groupies other than *mexicana* (Fig. 31): mean male forewing length and SE =  $14.81 \pm 0.14$  mm, range 14.0–15.6 mm,  $n = 15$ . Usually 14 or 15 nudum segments; on average (14.3), about one segment more than in fellow groupies (Table 1).

**Holotype.** ♂, MEXICO, OAXACA, El Vado-San Sebastian, ca 16° 53' N, 96° 53' W, 5500–6500 ft (1675–1980 m), 22 June 1992, J. Kemner; USNM.

**Paratypes.**  $n = 15$  ♂, all from MEXICO. OAXACA (all collected by J. Kemner and housed in USNM): same data, 6 ♂, J. M. Burns genitalia dissections X-3590, X-3591, X-3592; same data except 27 June 1992, 2 ♂; 3–13 mi (5–21 km) N Sola de Vega and road to Grutas de San Sebastian, 5500–6500 ft (1675–1980 m), 6 July 1991, 1 ♂; same data except 6500 ft (1980 m), 1 ♂, J. M. Burns genitalia dissection X-3241; road to Grutas de San Sebastian, 6500 ft (1980 m), 10 July 1991, 2 ♂, H. A. Freeman genitalia dissections H-1197, H-1202; road to Grutas de San Sebastian, ca 16° 37' N, 96° 57' W, 5500–6500 ft (1675–1980 m), 10 July 1991, 1 ♂, J. Kemner & Romack, J. M. Burns genitalia dissection X-3589. SINALOA: Loberas Summit, 5 mi (8 km) NE Potrerillos, 1820 m, parkland forest, 19 August 1973; 1 ♂, L. D. & J. Y. Miller, S. R. Steinhauser genitalia dissection SRS-2691, AME. SONORA: 13 mi (21 km) E El Novillo, 11 August 1985, 1 ♂, J. P. Brock, S. R. Steinhauser genitalia dissection SRS-1851, AME.

**Etymology.** *Quasimellana siblinga* is a sibling species.

*Quasimellana balsa* (Bell, 1942b:460, fig. 4), new combination  
(Figs. 31, 44, 45, 70, 71)

= *balsa freemani* (Steinhauser, 1974:20, figs. 53–56, 85, 86), new synonym, HT♂-AME.

HT♂-AMNH. Mexico (Sonora, Jalisco, Colima, Michoacán, Guerrero); Steinhauser (1974, 1975) reports this species from El Salvador. 17 ♂ 4 ♀ (14 ♂ 4 ♀).

See *siblinga* for definition of the male.

Much as in *mexicana* (Figs. 68, 69), the sclerotized lateral lobes of the lamella postvaginalis (on either side of the midventral, posteriorly directed, bristly projection) do not extend as far caudad (Figs. 70, 71) as they do in most species of *Quasimellana*; but the ductus bursae is remarkably short and oval (in ventral view [Fig. 70]), with an ostium (also somewhat oval) that opens far back at the base of the midventral, bristly projection, which is shorter and wider than it is in *mexicana* (see also Steinhauser 1974:fig. 86).

The subspecies *freemani* is not helpful. *Mellana balsa freemani* was described from six males and three females all from one locality (Santa Tecla) in El Salvador (Steinhauser 1974). When this short series was compared with the still shorter type series of *balsa*, amounting to four males from Guerrero, Mexico, it was said that "*freemani* males differ from typical *balsa* mainly in size and color" (Steinhauser 1974:22), the male genitalia being "essentially identical." In every large sample of a *Quasimellana* species (and sometimes even in small ones) I have seen too much variation in color and pattern to give weight to the two color differences offered. Though real and noteworthy, the larger size of El Salvador specimens does not warrant a formal name. By my measurements the type series of *balsa* is small, averaging 14.3 mm in forewing length (ranging from 13.7 to 14.6 mm); but my total Mexico sample of *balsa* ( $n = 16$ ), which includes those small types, is nearly a millimeter larger, averaging 15.04 mm (ranging from 13.7 to 15.7 mm) (Fig. 31). The El Salvador sample picks up where the Mexico sample leaves off and adds about another millimeter to the mean: according to Steinhauser (1974:22), the six *freemani* males average 16.2 mm (ranging from 15.8 to 16.5 mm). Elsewhere in *Quasimellana*, with enough *eulogius* to take good geographic subsamples, the forewings of 32 males from Honduras, Nicaragua, Costa Rica, and Panama averaged about half a millimeter more than those of 32 males from Mexico (Fig. 31). In *Autochthon cellus*, wing length rose strikingly from central Mexico to southern Mexico to Guatemala and El Salvador

(Burns 1984:10 and table 1). Skipper populations of a single species often increase in average wing length from north to south in the northern hemisphere (see tables and text in Burns 1964, 1984 for examples from *Erynnis* and *Wallengrenia*).

*Quasimellana mulleri* (Bell, 1942b:462, fig. 6),  
new combination  
(Figs. 31, 37, 38, 73)

HT♂-USNM. Mexico (Tamaulipas, Durango, Jalisco, Colima, Guerrero). 9 ♂ 5 ♀ (7 ♂ 3 ♀).

The body of the cornutus is wide, with numerous peripheral wrinkles (Figs. 37, 38); and the rounded dorsodistal end of the valva tends to develop a modest point antero-dorsally. Overall the female genitalia (Fig. 73) look most like those of *mexicana* (Figs. 68, 69); but the lateral lobes of the lamella postvaginalis extend well back as they do in most species of *Quasimellana*, while the midventral, posteriorly directed, bristly projection is about as delicate as it is in *andersoni* (Fig. 75), *myron* (Fig. 77), *verba*, *inconspicua*, and *angra* of the *sethos* group.

Freeman (1967) argued that *mulleri*, which Evans (1955) questioningly called a synonym of *eulogius*, is really a distinct species.

The *sethos* Group  
(Figs. 31, 36, 46–60, 74–77, 93–108)

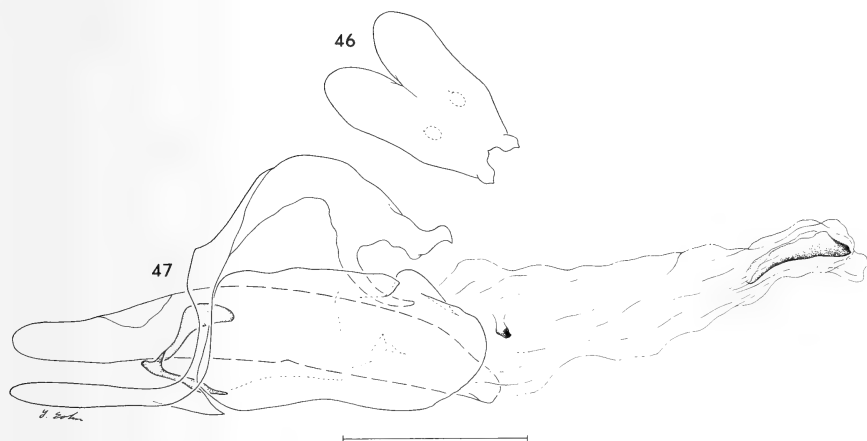
**Male genitalia.** *Juxta*: The juxta may be posterior (Figs. 47, 55) or anterior (Figs. 52, 57, 59) in location. The level of the twist in each lateral arm of the juxta is low (Figs. 47, 52, 55, 57, 59), as it is in the *eulogius* group (Figs. 41, 43, 45). *Cornutus*: The head-and-neck of the cornutus is relatively long and/or narrow (Figs. 36, 47, 49, 50, 52, 55, 57, 59, 60), it projects obliquely forward from the body of the cornutus (Figs. 36, 47, 49, 50, 52, 55, 59, 60), and its "dewlap" is finely crenulate (Figs. 47, 49, 50, 52, 55, 59, 60). (Among other species of *Quasimellana*, only *amicus* has a crenulate "dewlap.") The body of the cornutus is dorsally flattish to concave (at some angles, concavity gives a "swaybacked" look—Figs. 36, 49, 52, 55, 59). The tiny, secondary, vestigial cornutus is present (Figs. 47, 49, 52, 55, 57, 60), as it usually is in the *eulogius* group, except in the two known individuals of *pazina* (Fig. 50), the one of *sista* (Fig. 53), one of the examined males of *verba*, nearly half the examined males of *inconspicua* (Fig. 59), and most examined males of *myron*. *Vesica*: The everted vesica is relatively long (Figs. 47, 49, 50, 52, 53, 55, 57, 59, 60). *Valva*: On its inner surface, the valva has at least a rudimentary, but usually a well developed, dorsal process, which is unique among species of *Quasimellana* (Figs. 49, 50, 52, 53, 55, 57, 59, 60 [in these last two species, the dorsal process is short and extends mostly mediad, so it hardly shows in lateral view]). (The only males of the *sethos* group really lacking a dorsal process are two of the eight *nayana* examined, one of which appears in Fig. 47.) Although the distal end of the valva varies greatly, its basic pattern apparently is a pair of projections, one dorsal and the other more or less midcaudal. *Uncus*: The distal end of the uncus may be very well divided (Figs. 46, 48, 51) or undivided (Figs. 54, 56, 58). (Among other species of *Quasimellana*, only *amicus* has an undivided uncus.) In lateral view, the distal end of the uncus is only a little thicker than the distal end of the gnathos (Figs. 47, 49, 52, 55, 57, 59), as it is in the *eulogius* group (Figs. 41, 43, 45) and in *amicus* of the *nicomedes* group.

**Female genitalia.** The anterior apophyses are short (Figs. 74, 75) except in *sethos* (Fig. 76), where they are intermediate (females of several species are unknown). The corpus bursae is relatively long and narrow (Figs. 74–77).

**General features.** Sexual dimorphism is weak to strong. The species are small to large in size (Fig. 31).

**Distribution.** Extending from Mexico to Bolivia and Brazil, the *sethos* group (with 12 species) is equally North and South American.





FIGS. 46, 47. Male genitalia of *Quasimellana nayana* from Santo Domingo, 15 mi (24 km) SE Simojovel, Chiapas, MEXICO, 8–15 July 1958, J. A. Chemsak (X-2789) (USNM). Scale = 1.0 mm. **46**, Tegumen and uncus in dorsal view. **47**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

### The *nayana* Subgroup within the *sethos* Group (Figs. 31, 46, 47, 74)

**Male genitalia.** *Juxta*: The juxta is posterior in location (Fig. 47). *Cornutus*: The head-and-neck arises from the right side of the body of the cornutus. *Uncus*: The distal end of the uncus is very well divided, and the resultant uncus prongs are widely separated from each other (with a U-shaped gap) and somewhat divergent (Fig. 46). *Gnathos*: In lateral view, the gnathos is uniquely far below the uncus and uniquely short relative to the uncus (Fig. 47).

**Female genitalia.** The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is hypertrophied and the rounded lobes of the lamella postvaginalis that flank it are atrophied (Fig. 74) so that the usual size relationships between these parts (Figs. 68–73, 75–82) are reversed.

**General features.** Sexual dimorphism is strong. The species are medium sized (Fig. 31).

**Distribution.** The *nayana* subgroup (with 2 species) ranges from southern Mexico to Venezuela.

In a three-paper flurry, Bell (1941, 1942a, 1942b) described eight new species of what is now *Quasimellana*, seven of which are valid (*ricana* is a synonym of *meridiani* Hayward 1934). Bell put all of them in genus *Atrytone* except one: *aurora* went in *Zariaspes*, which is nowhere near *Atrytone*. Ironically, Bell (1942b:460–465) described *aurora* right after *balsa*, *mexicana*, and *mulleri*, with figures of male genitalia detailed enough to show the same (i.e., *Quasimellana*) kind of cornutus in all four species. Although *aurora* diverged from the other three (which are in the *eulogius* group) in the form of the tegumen, uncus,

and gnathos, as well as in the form of the valva, it rather resembled *nayana*, one of the *Atrytone* species Bell had described the year before. Evans (1955) misdetermined his only male of *aurora* as *nayana* and left *aurora* in *Zariaspes*, from which I am finally freeing it.

Both *aurora* and *nayana* came from southwestern Mexico. Steinhauser (1974) described them again from El Salvador as *Mellana tecla* and *M. tamana*.

*Quasimellana aurora* (Bell, 1942b:464, fig. 7), new combination  
(Figs. 31, 74)

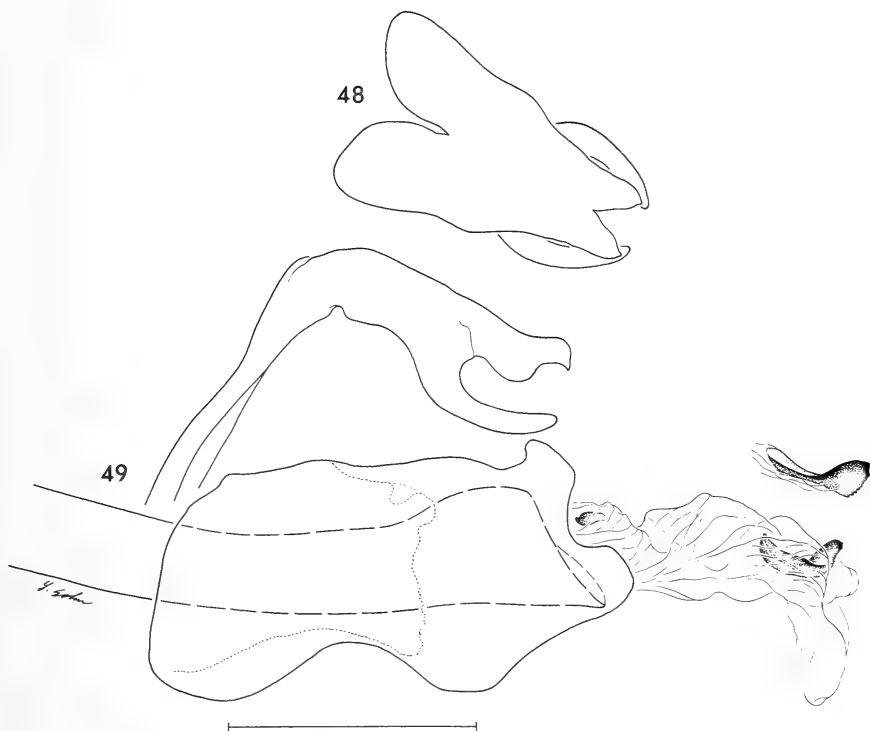
= *tecla* (Steinhauser, 1974:15, figs. 41, 42, 81), new synonym, HT♂-AME.

HT♂-AMNH. Mexico (Sinaloa, Jalisco, Colima, Guerrero, Oaxaca, Chiapas), El Salvador. 30 ♂ 2 ♀ (16 ♂ 2 ♀).

In dorsal view, the tegumen/uncus is narrower and the uncus prongs are closer together in *aurora* than in *nayana* (Fig. 46), while, in lateral view, the uncus prongs are nearly straight (i.e., almost in line with the rest of the tegumen/uncus) in *aurora*, rather than bent sharply upward as they are in *nayana* (Fig. 47). The valva of *aurora*, in lateral view, has short, blunt, but relatively narrow projections both dorsally and midcaudally, with the dorsal projection usually inclined a bit anterodorsally. Both valval projections in *nayana* are broader and more bluntly rounded (the midcaudal projection so much so, that it sometimes melts into a totally rounded caudal end, as in Fig. 47). The triangular middle process on the inner side of the valva is smaller in *aurora* than it is in *nayana* (Fig. 47). These two species are superficially very similar, the males with dorsal light areas that are more extensive, and usually more orange, than in most other species of *Quasimellana*; but, on an average, the light areas are slightly more extensive in *aurora* than in *nayana* (compare the *aurora* and *nayana* males in figs. 41, 42 and figs. 49, 50, respectively, in Steinhauser 1974:30). Two males of *aurora* from Colima, Mexico, are so extensively light, and their orange is so yellow, that they suggest some species of *Anatrytone*, as well as *Quasimellana imperfida*. Although both species are medium sized, *aurora* is a little larger than *nayana* (Fig. 31).

Genitalia can be deceitful even in published figures. In the lateral views accompanying Bell's original descriptions (Bell 1941:fig. 2, 1942b:fig. 7), the uncus prongs look straight not only in *aurora* (where they should) but also in *nayana* (where they should bend sharply upward). The uncus bend does not show in Bell's genitalic slide of the *nayana* holotype because the tegumen, uncus, and gnathos are mounted at an odd angle. The valva of *aurora* is poorly drawn in Bell (1942b:fig. 7) but well photographed in Steinhauser (1974:fig. 81). Evans's (1955:pl. 79, fig. M.25.1) caricature of the male genitalia of what he calls *nayana* actually depicts *aurora*; and Steinhauser's (1974:figs. 43, 44, 82) photos of a *tecla* (= *aurora*) female, and her genitalia, really relate to *eulogius*.

To match mates can be tricky, especially in strongly dimorphic species. I know from comparing series of *Quasimellana* females that the taxonomically important, midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis may vary greatly in size and shape among conspecific individuals. It certainly varies among the three females I have seen in the *nayana* subgroup (whose genitalia—with their ultrawide, midventral, bristly projection and small lateral lobes [Fig. 74]—are immediately distinct). Though all three females may belong to the same species, I am tentatively referring the two with shorter bristly projections (Fig. 74) to *aurora* and the one with the bristly projection twice as long (about as in Steinhauser 1974:fig. 84) to *nayana*. Even so, a large measure of individual variation remains since the bristly projection is considerably shorter and wider in the unfigured female of *aurora* than it is in the figured female (Fig. 74), and distally truncate, instead of rounded.



FIGS. 48, 49. Male genitalia of holotype of *Quasimellana noka* (what remains of Evans's dissection), locality unknown, (X-3457) (BMNH). Scale = 1.0 mm. **48**, Tegumen, uncus, and gnathos in dorsal view. **49**, Tegumen, uncus, gnathos, upper vinculum, left valva, and distal end of aedeagus, with vesica everted and cornuti stippled, in left lateral view (plus primary cornutus in profile).

*Quasimellana nayana* (Bell, 1941:1, fig. 2), new combination  
(Figs. 31, 46, 47)

= *tamana* (Steinhauser, 1974:18, figs. 49, 50, 83, 84), new synonym, HT♂-AME.

HT♂-AMNH. Mexico (Nayarit, Chiapas), Guatemala, El Salvador, Venezuela. 8 ♂ 1 ♀ (8 ♂ 1 ♀).

See *aurora*.

Ungrouped Species within the *sethos* Group  
(Figs. 31, 36, 48–57, 75, 76, 93–104)

This artificial assemblage of 6 species includes an obvious sister pair: *pazina* and *antipazina*.

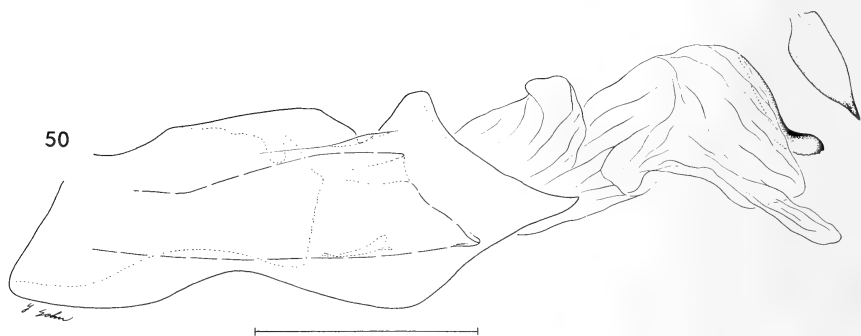


FIG. 50. Male genitalia of holotype of *Quasimellana pazina* (what remains of Evans's dissection) from Yungas and La Paz, 1000 m, BOLIVIA, 1902 (X-3460) (BMNH). Scale = 1.0 mm. Most of left valva and distal end of aedeagus, with vesica everted and cornutus stippled, in left lateral view (plus cornutus in dorsal view).

*Quasimellana noka* (Evans, 1955:357, pl. 79, fig. M.25.10),  
new combination  
(Figs. 31, 48, 49, 93, 94)

HT♂-BMNH. No locality. 1 ♂ (1 ♂).

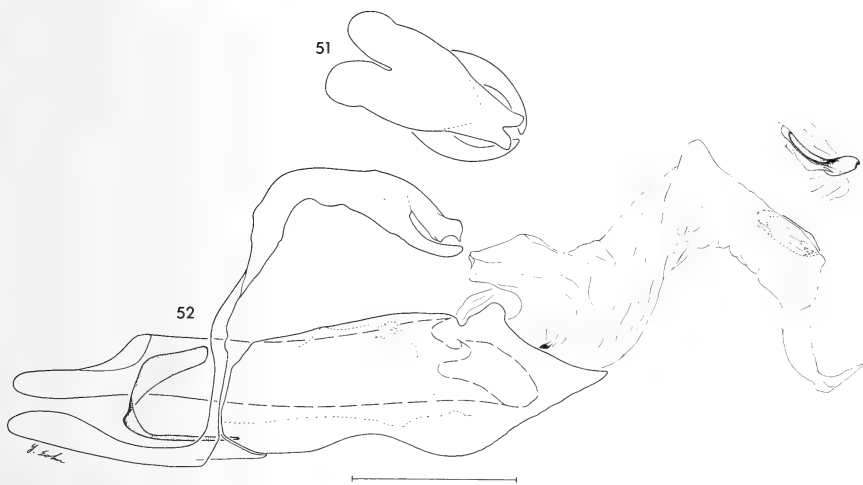
I can safely claim that this genitally peculiar species, known only from a dataless type, comes from somewhere in the neotropics. The valva of *noka* is unique: two narrow, rounded, posterodorsal and midcaudal projections extend not just dorsad and caudad but, at the same time, strongly mediad (Fig. 49). The valva lacks a triangular middle process on its inner side. Although the uncus is well divided (Fig. 48), the prongs are neither widely separated nor somewhat divergent as they are in the *nayana* subgroup (Fig. 46). Instead, they are much as in *pazina* and *antipazina* (Fig. 51), with a V-shaped (not U-shaped) intervening gap and just a hint of divergence. Since Evans's dissection wrecked the juxta, I cannot say whether it is posterior or anterior in location. Dorsally the light areas of the wings are neither extensive and orangy, as in *aurora* (Steinhauser 1974:fig. 41), *nayana* (Steinhauser 1974:fig. 49), *sista* (Fig. 99), and *andersoni* (Fig. 101), nor reduced and pale yellow, as in *inconspicua* and *angra* (Fig. 107). The result is an "average look" (Fig. 93), with yellow orange spots—the spotting less developed than in *pazina* (Fig. 95) but much as in *myron* and *verba* (Fig. 105). Ventrally a dirty, dull orangish shade runs over the hindwing and along the costa and across the apex of the forewing (Fig. 94).

*Quasimellana pazina* (Evans, 1955:357, pl. 79, fig. M.25.9),  
new combination  
(Figs. 31, 50, 95, 96)

HT♂-BMNH. Bolivia. 2 ♂ (2 ♂).

See *antipazina*.

Evans described *pazina* from a single male. Light areas (which are dorsally yellow orange to orange and ventrally yellower) are much more extensive in the second known male of *pazina* than they are in the first (the type, shown in Figs. 95, 96)—so much so,



FIGS. 51, 52. Male genitalia of holotype of *Quasimellana antipazina* from La Estrella, 1500 m, Cartago, COSTA RICA, 20 May 1979, G. B. Small (X-2592) (USNM). Scale = 1.0 mm. **51**, Tegumen, uncus, and gnathos in dorsal view. **52**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view (plus primary cornutus in profile).

that the second male will not key to *pazina* in Evans (1955). Dissection of the new male reveals that the juxta is anterior in location and confirms the fact that the uncus is divided. Evans (1955:pl. 79, fig. M.25.9) clearly showed a divided uncus in his trio of original genitalia figures; but the tegumen, uncus, gnathos, and vinculum of his dissected holotype have since been lost.

***Quasimellana antipazina*, new species**  
(Figs. 31, 51, 52, 97, 98)

HT♂-USNM. Costa Rica. 1 ♂ (1 ♂).

Superficially and dorsally much like *myron* and *verba*, with light areas reduced to discrete orange yellow spots (Fig. 97); ventral overscaling (narrowly along costa of forewing, broadly across apex of forewing, and all over the hindwing) not pale, cold, dull greenish as in those species but warm, yellowish brown (Fig 98). Light dashes on dorsal hindwing distal to cell reduced to only two, in spaces 3 and 4 (Fig. 97)—usually more in *myron* and *verba* (and other species). Much larger than *myron* and *verba*: lone male (forewing 17.0 mm) nearly attaining mean male forewing length of *mexicana*, the giant of *Quasimellana*, and exceeding the larger (16.4 mm) of two known males of *pazina* (Fig. 31). As in *pazina*, nudum of 15 segments (Table 1) and apiculus exceptionally long for *Quasimellana* (but *pazina* with better developed light areas dorsally, especially on hindwing [Fig. 95], and *pazina* bright yellow to orange yellow ventrally [Fig. 96], instead of yellowish brown). Genitalia (Figs. 51, 52) very like those of *pazina* (Fig. 50)—including juxta anterior in location—but divided uncus narrower, with each prong less massive in dorsal view, less elevated distally in lateral view, and proximally lacking ventrolateral swelling large enough to show in dorsal view; valva with dorsodistal projection (which extends dorsad and mediad) narrower (though with extended, sharp, midcaudal projection just as in *pazina* [compare Figs. 52 and 50]); and tiny, secondary, vestigial cornutus present.



FIG. 53. Male genitalia of holotype of *Quasimellana sista* (what remains of Evans's dissection) from VENEZUELA (X-3459) (BMNH). Scale = 1.0 mm. Most of left valva and distal end of aedeagus, with vesica everted and broken cornutus stippled, in left lateral view (plus broken cornutus in dorsal view).

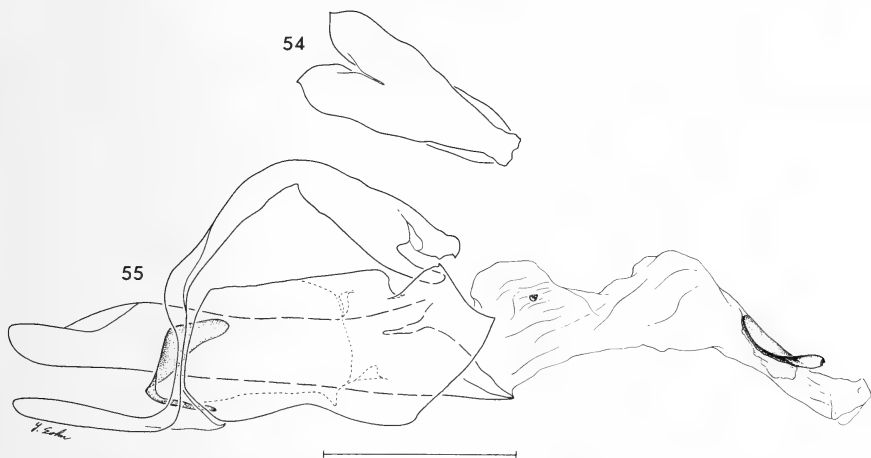
**Holotype.** ♂; COSTA RICA, CARTAGO, La Estrella, 1500 m, 20 May 1979, G. B. Small; J. M. Burns genitalia dissection X-2592; USNM.

**Etymology.** *Quasimellana antipazina* is the sister species and counterpart of *Q. pazina* in the opposite hemisphere (northern instead of southern).

*Quasimellana sista* (Evans, 1955:356, pl. 79, fig. M.25.5),  
new combination  
(Figs. 31, 53, 99, 100)

HT♂-BMNH. Venezuela. 1 ♂ (1 ♂).

Placing this species (or determining its *sista*) is extra difficult because the holotype is still the only specimen, Evans (1955:pl. 79, fig. M.25.5) provided just two of his usual three genitalic views (omitting the ventral view of the tegumen, uncus, gnathos, and distal end of the aedeagus), most of Evans's dissection of the genitalia is now missing, and the parts that remain (valva, aedeagus, cornutus) are broken (Fig. 53). Both the everted vesica and what there is of the cornutus clearly indicate the *sethos* group. For finer placement it would help to know whether the juxta is posterior or anterior, and the uncus, divided or undivided. Though the (incomplete) valva looks most like that of *andersoni* (Fig. 55), there are significant differences: the sharp, midcaudal projection points dorsad instead of caudad, the ventrodistal corner of the valva curves gently instead of angling sharply, and the triangular middle process on the inner side has disappeared (Fig. 53). Finally, *sista* lacks the tiny, secondary cornutus; and its big cornutus lacks the ventrally protruding sclerotization of *andersoni* (Fig. 55). Superficially, with extensive light areas and orange coloring, *sista* looks a lot like *andersoni*, *pazina*, *aurora*, and *nayana* (and it may be sympatric with *nayana*, since both occur in Venezuela—but no further locality data exist for *sista*). However, the orange in space 1b of the dorsal forewing essentially stays in the lower half of that space in *sista* (Fig. 99) while spreading the full height of that space in the other four species (Figs. 95, 101 and Steinhauser 1974:figs. 41, 49).



FIGS. 54, 55. Male genitalia of paratype of *Quasimellana andersoni* from Dos Amates, Veracruz, MEXICO, 15 January 1972, (X-3004) (Anderson collection). Scale = 1.0 mm. **54**, Tegumen, uncus, and gnathos in dorsal view. **55**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

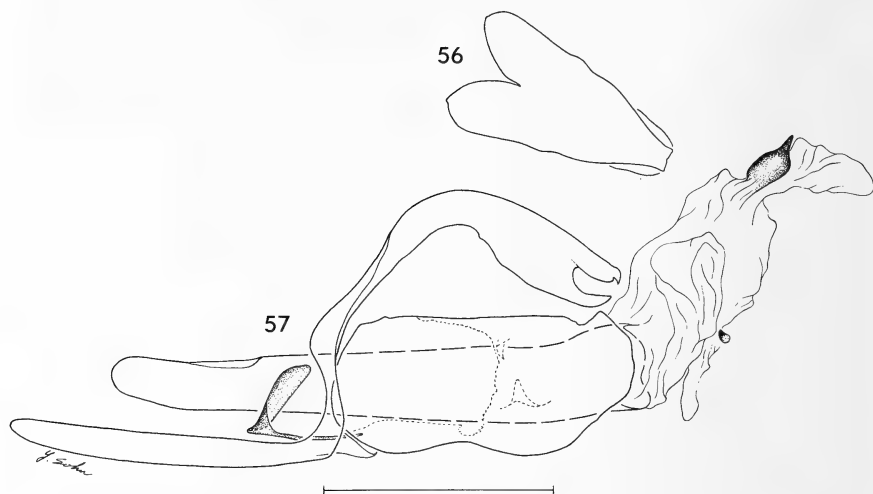
***Quasimellana andersoni*, new species**  
(Figs. 31, 54, 55, 75, 101–104)

HT♂-USNM. Mexico (Veracruz, Chiapas), Costa Rica. 8 ♂ 2 ♀ (8 ♂ 2 ♀).

Superficially very like *aurora* and especially *nayana* of *nayana* subgroup, with extensive, orange, light areas dorsally and ventrally in male and strong sexual dimorphism (Figs. 101–104). Near *nayana* in size, probably a little smaller on average (Fig. 31), so one of the smallest species of *Quasimellana*: mean male forewing length and SE =  $13.66 \pm 0.21$  mm, range 12.8–14.5 mm,  $n = 8$ ; but number of nudum segments (mean 14.8) maximum for *sethos* group (Table 1). Despite posterior juxta (Fig. 55), male genitalia highly distinct from *nayana* subgroup: tegumen/uncus long and narrow, with uncus undivided (Fig. 54); valva (Fig. 55) perhaps most like *sista* (qv) (Fig. 53; Evans 1955:pl. 79, fig. M.25.5), but also somewhat remindful of *myron*, *verba*, *pazina* (Fig. 50), and *antipazina* (Fig. 52) except for very short, unextended, sharp, midcaudal projection; body of cornutus with at least some ventrally protruding sclerotization (Fig. 55) and dorsally more concave than in other species of *Quasimellana*. Midventral, posteriorly directed, bristly projection from posterior margin of lamella postvaginalis, delicate (Fig. 75), about as in *myron* subgroup (Fig. 77) and *mulleri* of *eulogius* group (Fig. 73); outline of ostium bursae flask-shaped in ventral view (Fig. 75); anterior ductus bursae abruptly constricted to half the posterior width, in dorsal and ventral view (Fig. 75).

**Holotype**. ♂, MEXICO, VERACRUZ, Tapalapa, September 1971; J. M. Burns genitalia dissection X-3003; USNM.

**Paratypes**.  $n = 7$  ♂ 2 ♀. MEXICO, VERACRUZ: Dos Amates, 15 January 1972, 1 ♂, J. M. Burns genitalia dissection X-3004, collection of R. A. Anderson; Catemaco, December 1963, 3 ♂, T. Escalante, H. A. Freeman genitalia dissection H-257, J. M. Burns genitalia dissections X-3644, X-3645, AMNH; same data except October 1965, 1 ♂, S. R. Steinhauser genitalia dissection SRS-2702, AME. MEXICO, CHIAPAS, Santa Rosa, Comitán, September 1963, 1 ♂ 2 ♀, T. Escalante, H. A. Freeman genitalia dissection H-64, J. M. Burns genitalia dissections X-3642, X-3643, AMNH. COSTA RICA, HEREDIA, 3.8 km N Santa Clara, 5 September 1987, 1 ♂, G. & A. Austin, S. R. Steinhauser genitalia dissection SRS-2957, collection of G. T. Austin.



FIGS. 56, 57. Male genitalia of *Quasimellana sethos* from Paraíso, Canal Zone, PANAMA, 27 April 1982, S. S. Nicolay (X-2596) (USNM). Scale = 1.0 mm. **56**, Tegumen, uncus, and gnathos in dorsal view. **57**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

**Etymology.** I am pleased to name this species for Richard A. Anderson who generously and patiently provided large numbers of *Quasimellana* from his collection.

*Quasimellana sethos* (Mabille, 1889:173, fig. 2),  
new combination  
(Figs. 31, 36, 56, 57, 76)

Panama, Colombia, Ecuador; Evans (1955) also records a total of three males from Nicaragua and Venezuela. 21 ♂ 3 ♀ (6 ♂ 2 ♀).

This, the smallest species of *Quasimellana* (Fig. 31), is what Godman (1900) called *Atrytone helva* and Evans (1955), *Mellana helva*. Godman (1900:494), on examining the female type of *Pamphila helva* Möschler (1876) from Surinam and the male type of *P. sethos* Mabille (1889) from Chiriquí (western Panamá), erroneously judged them conspecific and applied the older name. Godman (1900:pl. 94, figs. 25–29) figured, in color, “the type of *P. sethos*, a male, from Chiriquí, and a female from Coatepec [Veracruz, Mexico], agreeing with the type of *P. helva*,” and, in black and white, the male genitalia. The genitalic figure represents this species best (even a *Quasimellana*-style cornutus shows). With orange yellow spots, the figured female looks much like the male; but she has well developed subapical spots on the forewing in spaces 6, 7, and 8, where the male has only a small point in space 6. The trouble is that this species of *Quasimellana* (like many others) exhibits strong sexual dimorphism in which the spots of the female are white instead of yellow to orange, and are less well expressed than those of the male. I have carefully studied the original descriptions of *Pamphila helva* (Möschler 1876), described from a male as well as a female, and *P. sethos* (Mabille 1889), described from a single male. Each description includes critical verbal detail plus a good black and white figure of the adult. Without question, *sethos* is the species long designated as *helva*; and *helva* is not a species of *Quasimellana*.

The saccus of *sethos* is exceptionally long for *Quasimellana*—from slightly shorter to slightly longer (Fig. 57) than the valva. In lateral outline the valva (Fig. 57) is the simplest



of the *sethos* group—about as plain as those of the *eulogius* group (Figs. 41, 43, 45). The body of the cornutus is peripherally wrinkled (Fig. 36)—but much less densely than in *mulleri* (Figs. 37, 38) of the *eulogius* group. The juxta is anterior and the uncus undivided (Figs. 56, 57), a combination of character states that relates to the upcoming *myron* subgroup of four species (qv). The midventral, caudally directed projection from the posterior margin of the lamella postvaginalis is just a suggestion of its usual self (Fig. 76). Dorsally, in color and pattern, the dimorphic sexes of the diminutive *sethos* resemble those of the larger *myron* and *verba*, except that *sethos* males express a slender spot in space 4 usually missing from *myron/verba*. Ventrally, in fresh specimens of *sethos*, a slight greenish cast—over orange yellow in males and over brownish yellow in females—somewhat suggests the dull but more pronounced ventral greenish often visible in the *myron* subgroup.

### The *myron* Subgroup within the *sethos* Group (Figs. 31, 58–60, 77, 105–108)

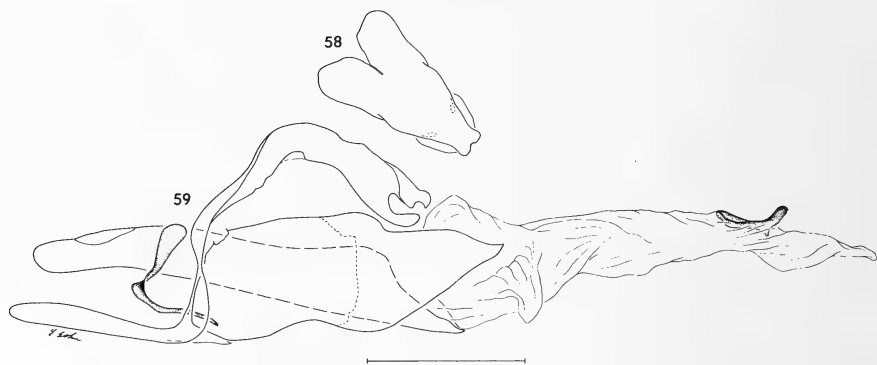
**Male genitalia.** *Juxta*: The juxta is anterior in location (Fig. 59). *Valva*: The valva has at least a long, sharp midcaudal projection that points caudad, and often a little mediad (Figs. 59, 60). *Uncus*: The distal end of the uncus is undivided, though usually a bit bilobed (Fig. 58).

**Female genitalia.** The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is delicate (Fig. 77), about as in *andersoni* (Fig. 75) and *mulleri* (Fig. 73). The posterior part of the sclerotized ductus bursae usually extends farther caudad, bringing the ostium bursae closer to the midventral, bristly projection (Fig. 77). The anterior part of the sclerotized ductus bursae has a central, longitudinal, unsclerotized zone (Fig. 77).

**General features.** Male spotting varies from average to much reduced, with many males dark enough that the sexual dimorphism typical of *Quasimellana*, though present, is not striking. Ventral overscaling in both sexes often gives a pale, dull greenish cast. The species are medium sized to small (Fig. 31).

**Distribution.** The *myron* subgroup (with 4 species) ranges from Mexico to Bolivia and Brazil.

Evans (1955) treated three of the four taxa in this subgroup (*myron*, *verba*, and *inconspicua*) as subspecies of *myron*, describing the fourth (*angra*) as a separate species. Though all four are closely related, male genitalia show conclusively that two pairs of sister taxa are involved: *myron* and *verba*, on the one hand, and *inconspicua* and *angra*, on the other. The distal end of the valva in *myron* and *verba* has a major dorsal projection—totally lacking in *inconspicua* and *angra* (Figs. 59, 60)—which extends dorsad and mediad so that the valva as a whole resembles that of *pazina* and *antipazina* (Figs. 50, 52). Also, the dorsal process on the inner surface of the valva is long and conspicuous (as in most members of the *sethos* group) in *myron* and *verba* but short and inconspicuous in *inconspicua* and *angra* (Figs. 59, 60). Female genitalia support this grouping, though less showily: the posterior part of the ductus bursae is much longer than the anterior part in *myron* and *verba* (Fig. 77) but only a little longer in *inconspicua* and *angra*.



FIGS. 58, 59. Male genitalia of *Quasimellana inconspicua* from Puyo, 1000 m, Pastaza, ECUADOR, 19 October 1989, S. S. Nicolay (X-2826) (USNM). Scale = 1.0 mm. **58**, Tegumen, uncus, and gnathos in dorsal view. **59**, Complete genitalia (minus right valva), with vesica everted and juxta and cornutus stippled, in left lateral view.

(I will say nothing further about females within the *myron* subgroup because sound interspecific differences in genitalia and external appearance are not evident among the few specimens at hand.)

Although males of *myron* and *verba* are not difficult to recognize as a unit, they are hard to separate from each other. Evans (1955) described *verba* (from Costa Rica, Colombia, Ecuador, and Guyana) as a southern subspecies of *myron* (from Mexico, Nicaragua, and Costa Rica). But distinguishing characters neither hold completely nor neatly divide geographically. All things considered, these skippers look more like overlapping species than subspecies. A quick and easy alternative would be a single, too variable, species, at least as dissatisfying as *eulogius* (and unfortunately, for supplemental analysis, far rarer in collections). The *myron/verba* complex now appears to range from central Mexico to southern Brazil.

By contrast, *inconspicua* and *angra* are strictly South American, with *inconspicua* western (Ecuador to Bolivia) and *angra* to the east. Though their genitalia look the same and their wings look similarly dark, they differ enough in color, pattern, and size (Fig. 31) to warrant specific rank. Since Evans's (1955:358) lists of specimens examined include an *inconspicua* male from "Chanchamayo," Peru, and an *angra* male from "Perene," Peru, since both names refer to the same general collecting area, and since both skippers live at low elevation (even the western *inconspicua* is known only from 250–1000 m), *inconspicua* and *angra* may well be in contact or sympatric.

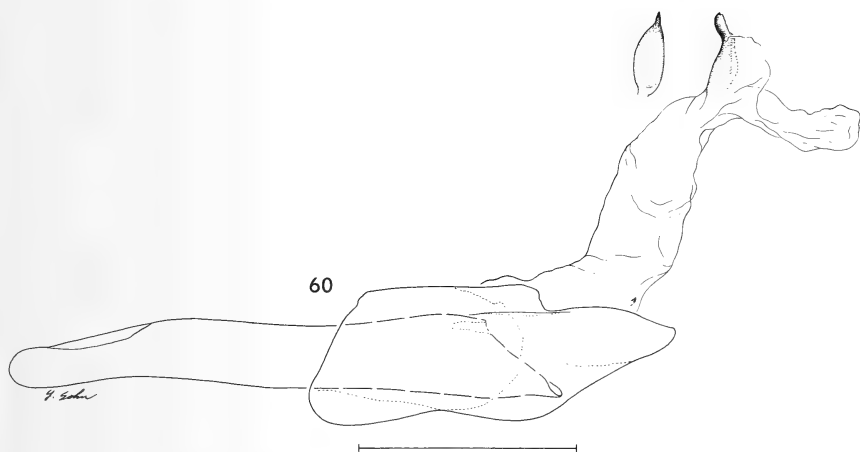


FIG. 60. Male genitalia of holotype of *Quasimellana angra* (what remains of Evans's dissection) from Pará, BRAZIL, H. W. Bates (X-3461) (BMNH). Scale = 1.0 mm. Left valva and aedeagus, with vesica everted and cornuti stippled, in left lateral view (plus primary cornutus in dorsal view).

*Quasimellana myron* (Godman, 1900:493, pl. 94, figs. 20–24),  
new combination  
(Figs. 31, 77)

Mexico (San Luis Potosí, Veracruz, Guerrero, Oaxaca, Quintana Roo), Guatemala, Honduras, Nicaragua, Costa Rica, Panama. 16 ♂ 5 ♀ (9 ♂ 4 ♀).

The dorsodistal projection of the valva is broader and distally rounder than it is in *verba*, and the valva has no middle process on its inner surface (see Evans 1955:pl. 79, fig. M.25.12 *myron*). The secondary, vestigial cornutus is usually absent (present in two males from Oaxaca, Mexico, but smaller than it is in *verba*). Male spot development in *myron* and *verba* is generally about average to somewhat reduced (Figs. 105, 106); but, in the specimens at hand (as in any appreciable series of *Quasimellana*), it varies considerably. Evans's (1955) observation that the yellow dorsal markings of the male are paler in *myron* and darker in *verba* appears valid but ever so subtle. I find the yellow spot in space 2 of the dorsal forewing more helpful: it tends to be rectangular (often squarish), with its inner edge more or less vertical, in males of *myron* but more nearly triangular (and wider), with its inner edge oblique, in males of *verba* (Fig. 105).

*Quasimellana verba* (Evans, 1955:358, pl. 79, fig. M.25.12),  
new combination  
(Figs. 31, 105, 106)

HT♂-BMNH. Mexico (San Luis Potosí, Yucatán), Panama, Colombia, Venezuela, Ecuador, Brazil (São Paulo). 12 ♂ 3 ♀ (12 ♂ 1 ♀).

The dorsodistal projection of the valva is narrower and distally more pointed than it is in *myron*, and the valva usually has a middle process on its inner surface (see Godman 1900:pl. 94, fig. 22 and Evans 1955:pl. 79, fig. M.25.12 *verba*)—but that process is small in three males from Mexico and Panama and absent in two males from Ecuador and Brazil. The secondary, vestigial cornutus is usually present (absent in the male from

Brazil). See *myron* for slight average differences between *myron* and *verba* in the external appearance of males.

*Quasimellana inconspicua* (Hayward, 1950a:465, fig. 5),  
new combination  
(Figs. 31, 58, 59)

HT♂-IML. Ecuador, Peru, Bolivia. 8 ♂ 2 ♀ (8 ♂ 1 ♀).

Spotting is so reduced in males of both *inconspicua* and *angra* that they look mostly dark. Their dorsal forewing bears a total of three small yellow spots in the lower part of space 1b and in spaces 2 and 3. Even though *inconspicua* is the larger species, averaging more than a millimeter longer than *angra* in wing length (Fig. 31), its spots are smaller and relatively diffuse—much less sharply defined than they are in *angra* (Fig. 107). Moreover, in *inconspicua* the yellow of these spots is a little paler; and the spot in space 3 is slightly distad of the spot in space 2, whereas in *angra* the spot in space 3 slightly overlaps the spot in space 2 (Fig. 107). Ventrally, males of *inconspicua* are darker and vaguely greenish brown when fresh, whereas *angra* males are lighter and somewhat yellowish brown. For whatever it may be worth with such small numbers, I note that the secondary, vestigial cornutus is absent in nearly half the dissected males of *inconspicua* (Fig. 59) but present in all four dissected males of *angra* (Fig. 60).

Specimens of *inconspicua* have been misdetermined as *pandora*, a superficially similar species or subspecies of *Quasimellana* in the *nicomedes* group and a very close sister of *meridiani*. See *meridiani* for a discussion of external differences between *inconspicua* and *pandora*.

*Quasimellana angra* (Evans, 1955:358, pl. 79, fig. M.25.13),  
new combination  
(Figs. 31, 60, 107, 108)

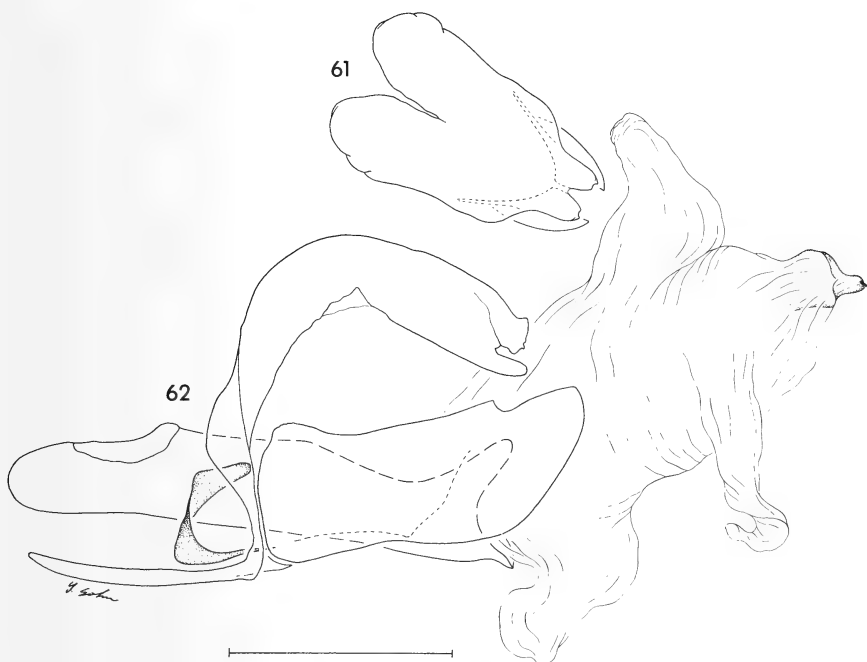
HT♂-BMNH. French Guiana, Brazil (Pará, Maranhão, Pernambuco, Bahia, Minas Gerais, Rondônia); Evans (1955) also lists one male each from Venezuela, Ecuador, and Peru. 6 ♂ 4 ♀ (4 ♂ 2 ♀).

See *inconspicua*.

This is the second smallest species of *Quasimellana*, exceeding only *sethos* (Fig. 31).

The *nicomedes* Group  
(Figs. 31, 34, 35, 39, 61–67, 78–82, 109–112)

**Male genitalia.** *Juxta*: As in some members of the *sethos* group, the juxta is anterior in location (Figs. 62, 65, 67); but the level of the twist in each lateral arm of the juxta is high (Figs. 39, 62, 65, 67), not low as it is in all other species of *Quasimellana* (Figs. 41, 43, 45, 47, 52, 55, 57, 59). *Cornutus*: The head-and-neck of the cornutus is short; it rises almost vertically from the body of the cornutus (Figs. 34, 35, 62, 65, 67). No member of the *nicomedes* group has the tiny, secondary, vestigial cornutus that usually occurs in other species of *Quasimellana*. *Vesica*: The everted vesica is relatively short, fat, and irregular (Figs. 62, 65, 67). *Valva*: The valva has neither a middle process nor a dorsal process on its inner surface (Figs. 62, 65, 67) (one or both processes are present in other species of *Quasimellana*). Distally the valva terminates in one or two dorsally directed, sharp points (Figs. 65, 67), except in *fieldi* (Fig. 62). *Uncus*: In lateral view, the distal end of the uncus is much thicker than the distal end of the gnathos (Figs. 62, 65, 67), except in *amicus* where (as in all other species of *Quasimellana*) the uncus is only a little thicker than the gnathos. Again, in lateral view, the uncus is usually (but not always) a little shorter than the gnathos (Figs. 62, 65, 67), except in *amicus*. *Tegumen*: In dorsal view the tegumen generally tapers more abruptly to the uncus (Figs. 61, 63, 64, 66) than it does in other species.



FIGS. 61, 62. Male genitalia of *Quasimellana fieldi* from San Salvador, EL SALVADOR, 29 December 1953, M. Salazar (X-2589) (USNM). Scale = 1.0 mm. **61**, Tegumen, uncus, and gnathos in dorsal view. **62**, Complete genitalia (minus right valva), with vesica everted and juxta and cornutus stippled, in left lateral view.

**Female genitalia.** The ductus bursae extends caudad ventrally but not laterally to form a unique scoop beneath the ostium bursae (Figs. 78–82). At its anterior end the sclerotized ductus bursae is longitudinally grooved and more or less expanded (Figs. 78–82). The anterior apophyses are neither long (as in the *eulogius* group) nor short (as in the *sethos* group). The only species outside of the *nicomedes* group with anterior apophyses of intermediate length are *sethos* and (in some individuals) *balsa*. The corpus bursae is relatively short and fat (Figs. 78–82), though less so in *fieldi*.

**General features.** Sexual dimorphism runs the gamut from nonexistent (*amicus*), through weak (*nicomedes*, *meridiani*, and presumably *pandora*), to strong (*imperfida*, *mielkei*, and *fieldi*); color pattern, from mostly dark (*meridiani* and especially *pandora*), through roughly half-and-half (*amicus* and *nicomedes*), to mostly light (in the predominantly yellow orange males of *fieldi*, *mielkei*, and especially *imperfida*). The species are small to medium in size (Fig. 31).

**Distribution.** Although the *nicomedes* group (with 7 species) extends from Mexico to Argentina, it is mainly South American.

### *Quasimellana amicus* (Bell, 1942a:2, fig. 3), new combination (Figs. 31, 78)

HT♂-AMNH. Ecuador. 8 ♂ 4 ♀ (5 ♂ 3 ♀).

Superficially this smallish species (Fig. 31) seems out of place in *Quasimellana* because females look just like males, the discal spotband (yellow orange) runs boldly and contin-

uously (cut by dark veins) up the forewing from space 1b to space 6 (or rarely 7) without the usual break in space 5 (distal to the upper half of the cell), and the ventral hindwing flaunts a dark border (interrupted by yellow in space 1c). This is the sole member of the *nicomedes* group in which the uncus is undivided and (in lateral view) only a little thicker than the gnathos. The long, low valva ends distally in a single, dorsally (and medially) directed, sharp point. The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is exceptionally delicate and long (extending far caudad of the paired, sclerotized, lateral lobes that flank it); its base is not quite hidden, in ventral view, by the posterior edge of the ventral scoop of the ductus bursae; and the longitudinally grooved, anterior end of the sclerotized ductus bursae is diagonal, slanting sharply forward (at about 45°) from right to left (Fig. 78).

*Quasimellana fieldi* (Bell, 1942a:2, fig. 4), new combination  
(Figs. 31, 34, 39, 61, 62)

= *montezuma* (Freeman, 1969:41, pl. 13, figs. 5–8; pl. 15, fig. 10), new synonym, HTδ-AMNH.

HTδ-USNM. Mexico (San Luis Potosí), Guatemala, El Salvador, Nicaragua; Evans (1955) gives Costa Rica. 54 ♂ 13 ♀ (10 ♂ 3 ♀).

The only North American species of the *nicomedes* group, *fieldi* superficially resembles members of the *eulogius* group (especially *mexicana*, *eulogius*, and *balsa*) inhabiting the same general region. The long, low valva comes dorsodistally to a blunt or vaguely pointed end (Fig. 62)—not a sharp point as in *amicus*. The uncus prongs (in dorsal view) are short, parallel, and more or less rounded at their distal ends (Fig. 61). The body of the cornutus is large and mostly flat (Figs. 34, 62). The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is medium in length (extending a little caudad of the paired, sclerotized, lateral lobes that flank it) and about as wide as it is in *mielkei* (Fig. 81) or *meridiani* (Fig. 82) to considerably wider. The longitudinally grooved, anterior end of the sclerotized ductus bursae is diagonal, much as it is in *amicus* (Fig. 78), but it slants forward from right to left even more steeply than in that species. (See Steinhauser 1974:fig. 87 for a photograph of the female genitalia of *fieldi* in ventral view.)

When Freeman (1969) described *montezuma* (which is synonymous with *fieldi*), he grouped it with what he called its “nearest relatives”—*nayana* and *mulleri*—in a “*nayana* complex,” based only on a few similarities in external appearance. In reality, these three species are not even close, each belonging in a different one of the three species groups of *Quasimellana*.

*Quasimellana nicomedes* (Mabille, 1883:LXX), new combination  
(Figs. 31, 35, 79, 80)

= *monica* (Plötz, 1886:98), new synonym, HT♀-ZMHB.

HTδ-ZMHB. Brazil (Paraná, Santa Catarina); Evans (1955) gives localities to the north in the neighboring states of São Paulo and Rio de Janeiro. 4 ♂ 4 ♀ (3 ♂ 3 ♀).

In the modest sexual dimorphism of *nicomedes*, the female expresses spots almost as well as the male, and her spots are a malelike yellow orange (not whitish and semihyaline on the forewing as they are in most species of *Quasimellana*). The long, low valva comes dorsodistally either to a single, sharp, dorsally directed point, as in *amicus*, or to two such points, as in *imperfida*, *mielkei* (Fig. 65), *pandora* (Fig. 67), and *meridiani*—but in *nicomedes* the points are a little closer together, and the distal point is higher than the proximal point instead of the other way around. The uncus prongs (in dorsal view) are very short, barely divergent, and truncate at their distal ends. The body of the cornutus is narrow and highly convex (Fig. 35). The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis (Figs. 79, 80) is delicate and long, extending somewhat caudad of the paired, sclerotized, lateral lobes that flank it—but not as far as in *amicus* (Fig. 78).

### *Quasimellana imperfida*, new species (Figs. 31, 63)

HTδ-USNM. Brazil (Mato Grosso, Goiás), Bolivia; Evans (1955) also lists Colombia and Paraguay under the name *Mellana perfida*. 4 ♂ 2 ♀ (4 ♂ 2 ♀).

I have scrutinized the type (♂-ZMHB), its genitalia (X-3763), and the original description of *perfida* Möschler (1878:221) and found that it is a species of *Anatrytone* and that what everyone is currently calling *Mellana perfida* is an undescribed species of *Quasimellana*.

See *mielkei*. Size similar to *mielkei*, maybe a little smaller (Fig. 31): mean male forewing length 15.4 mm, range 14.8–16.2 mm,  $n = 4$ ; mean female forewing length 16.8 mm, range 16.5–17.0 mm,  $n = 2$ . Nudum 14 or, usually, 15 segments (Table 1).

Externally, the light males of *imperfida* suggest males of *Anatrytone*—especially *A. perfida* or some combination of that species and *A. logan*. *Quasimellana imperfida* is a close sister to *mielkei* (qv); and these two are related, on the one hand, to the sisters *meridiani*/*pandora* and, on the other, to *nicomedes* (qv). The tegumen, uncus, and gnathos of *imperfida* (Fig. 63) are about as in *nicomedes*, while the cornutus is about as in *meridiani* and *pandora* (Fig. 67), i.e., with the body slightly less narrow and rather less highly convex (flatter) than in *nicomedes*. In lateral view the valva is not quite as low as in *fieldi* (Fig. 62) and especially *nicomedes* and *amicus*; in this regard, it is much like that of *meridiani* and *pandora* (Fig. 67) but longer. The female genitalia of *imperfida* are similar to those of *meridiani* (Fig. 82) and presumably *pandora*.

**Holotype.** ♂; BRAZIL, MATO GROSSO, Colegio Buriti, Chap. Guimarães, 700 m, 26 May 1969, S. S. Nicolay; S. S. Nicolay genitalia dissection H435 (left valva missing); USNM.

**Paratypes.**  $n = 3$  ♂ 2 ♀. BRAZIL: MATO GROSSO: Nivac, 1 ♂, J. M. Burns genitalia dissection X-3462, collection of O. H. H. Mielke; Buriti, Chapada dos Guimarães, 600 m, 27 June 1972, 1 ♀, Mielke & Brown, X-3463, specimen number DZ 3519 in UFPR; Cáceres, 7–9 February 1985, 1 ♂, C. Elias, X-3116, DZ 3513 in UFPR; GOIÁS, Goiás Velho, 25 February 1979, 1 ♀, Gifford, X-3464, DZ 3521 in UFPR. BOLIVIA, Chiquitas, 1 ♂, X-3764, ZMHB.

**Etymology.** *Quasimellana imperfida* simply is *not perfida*. Ever since Evans (1955), it has been going under the name *Mellana perfida*; but *perfida* is really a superficially similar looking species of *Anatrytone* (see p. 286).

### *Quasimellana mielkei*, new species (Figs. 31, 64, 65, 81, 109–112)

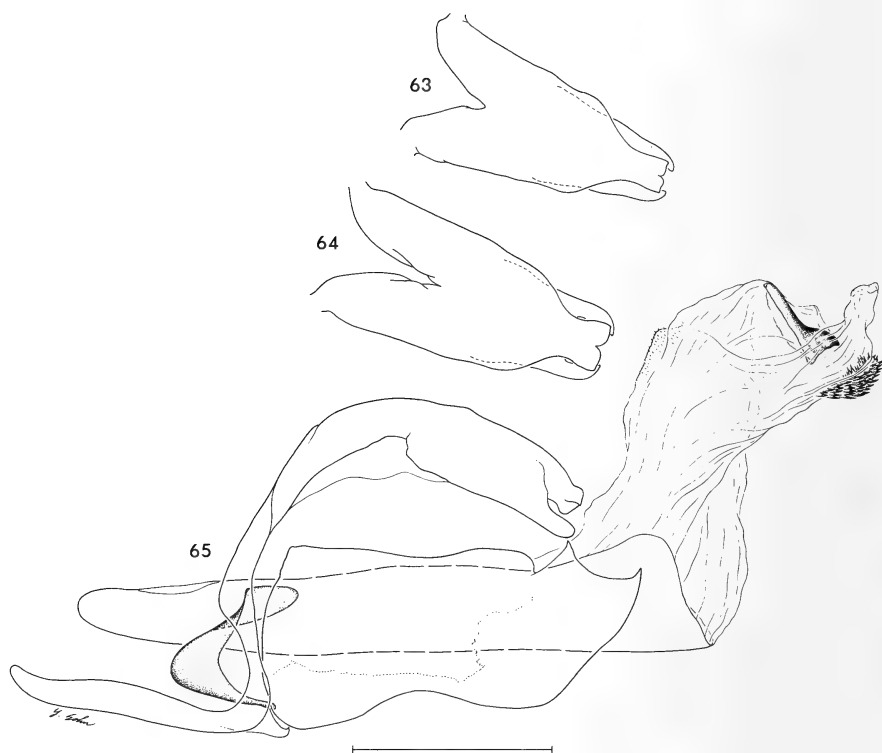
HT♂-UFPR. Brazil (Minas Gerais). 1 ♂ 1 ♀ (1 ♂ 1 ♀).

Close sister to *imperfida*. Sexual dimorphism strong (Figs. 109, 111), as in *imperfida* and *fieldi*. Wings fuller than in *imperfida*. Facies much as in *imperfida*, but dorsally, in male, extensive light areas of wings more orange (*imperfida* yellow), and transition between broad, light areas and narrow, dark, outer borders less hard and sharp; dorsally, in female, semihyaline spot in cell of forewing double (Fig. 111) instead of single as in *imperfida* (with so little material, this difference perhaps nothing more than individual variation); ventrally, in both sexes, dark ground color evident through thin, light over-scaling (Figs. 110, 112)—wings ventrally not almost all bright yellow as in *imperfida*. Genitalia in both sexes (Figs. 64, 65, 81) like those of *imperfida* (including small, flexible, well sclerotized, conspicuous, and coarsely spinulose scouring-pad cornutus in male [Fig. 65], not present in other species of *Quasimellana*) except uncus slightly wider in dorsal view (compare Figs. 64 and 63), aedeagus somewhat stouter, and ductus bursae slightly wider in ventral or dorsal view. Size similar to *imperfida*, maybe a little larger (Fig. 31): forewing length of male 16.0 mm; of female 17.0 mm. Nudum long—16 segments in both specimens.

**Holotype.** ♂; BRAZIL, MINAS GERAIS, Diamantino, November 1977, Sakakibare; J. M. Burns genitalia dissection X-3119; specimen number DZ 3515 in UFPR.

**Paratype.** ♀; same data; X-3120; DZ 3514 in UFPR.

**Etymology.** I am delighted to name this species for Olaf H. H. Mielke who has enormously increased our knowledge of neotropical skippers and has generously lent much helpful material.



FIGS. 63–65. Male genitalia of paratype of *Quasimellana imperfida* from Cáceres, Mato Grosso, BRAZIL, 7–9 February 1985, C. Elias (X-3116) (UFPR) and of holotype of *Q. mielkei* from Diamantino, Minas Gerais, BRAZIL, November 1977, Sakakibare (X-3119) (UFPR). Scale = 1.0 mm. **63**, Tegumen, uncus, and gnathos of *imperfida* in dorsal view. **64**, Tegumen, uncus, and gnathos of *mielkei* in dorsal view. **65**, Complete genitalia of *mielkei* (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

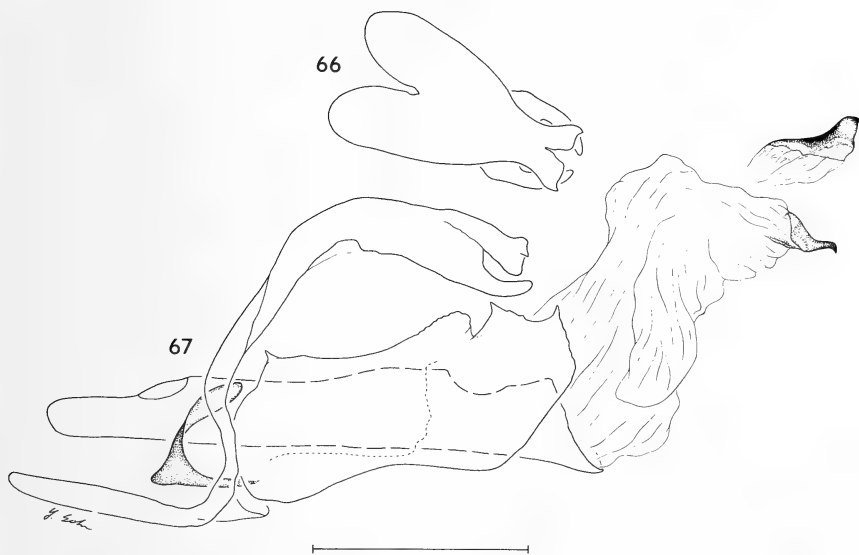
*Quasimellana meridiani* (Hayward, 1934:117, pl. 5, fig. 16),  
new combination  
(Figs. 31, 82)

= *ricana* (Bell, 1941:1, fig. 1), HT♂-AMNH.

Brazil (Paraná), Paraguay, Argentina (Misiones). 4 ♂ 1 ♀ (3 ♂ 1 ♀).

Though genitally close to the sisters *imperfida* and *mielkei*, sisters *meridiani* and *pandora* depart widely from them superficially: wings are relatively elongate and narrow (much as in various species of *Panoquina*), and are mostly blackish brown above. Males of *meridiani* are dorsally darkened enough to resemble females of *imperfida*, while males of *pandora*—their forewings usually with small yellow orange spots only in spaces 1b, 2, and 3—are so dark that they look like males of *inconspicua* of the *sethos* group. (However, spots in *pandora* are more orange than they are in *inconspicua*; the spot in space 3 is more distad of the spot in space 2 in *pandora* than it is in *inconspicua*; and the spot in





FIGS. 66, 67. Male genitalia of *Quasimellana pandora* from Rio Xingu Camp, 52° 22' W, 3° 39' S (first jungle stream trail 1, malaise trap day and night collection), ca 60 km S Altamira, Pará, BRAZIL, 2–8 October 1986, P. Spangler and O. Flint (X-2673) (USNM). Scale = 1.0 mm. **66**, Tegumen, uncus, and gnathos in dorsal view. **67**, Complete genitalia (minus right valva), with vesica everted and juxta and cornutus stippled, in left lateral view (plus cornutus in profile).

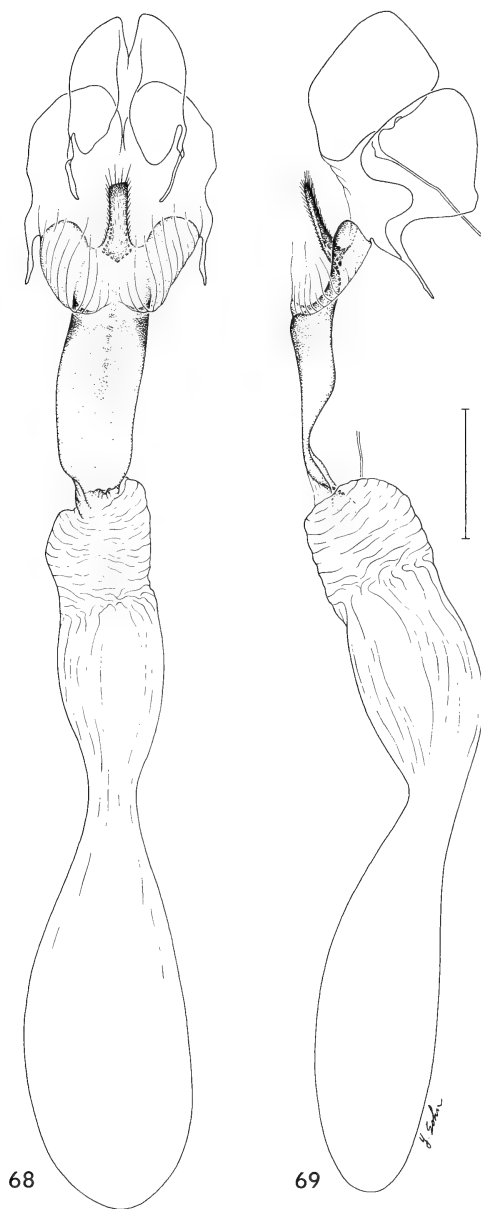
space 1b is, in *pandora*, often a sort of **V** on its side, spanning the height of space 1b, instead of a mere dot or bar, always limited to the lower part of that space, as it is in *inconspicua*. Moreover, males of *meridiani* and *pandora* average about a millimeter longer in the forewing than do males of *inconspicua* [Fig. 31]). Spotting in the female of *meridiani* is reduced from that in the male, but the spots are still a pale yellow orange; the female of *pandora* is unknown (spots in the female of *inconspicua* are whitish). Ventrally males of *meridiani* are mostly yellow but duller than in *imperfida*, and males of *pandora* are duller still (especially in Ecuador). The uncus prongs of *meridiani* and *pandora* are higher and wider than they are in other members of the *nicomedes* group: in left lateral view, the rounded, ventral lobe of the left prong projects exceptionally far downward (Fig. 67); in dorsal view, the prongs are truncate but distinctly divergent, usually with a good, triangular notch between them (Fig. 66). The valva (Fig. 67) is about as in *imperfida* and *mielkei* (Fig. 65) but shorter. The female genitalia (Fig. 82) are similar to those of *imperfida* and *mielkei* (Fig. 81), but the midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is a little heavier and wider, at least in *meridiani* (the female of *pandora* is unknown).

*Quasimellana pandora* (Hayward, 1940:867, fig. 20),  
new combination  
(Figs. 31, 66, 67)

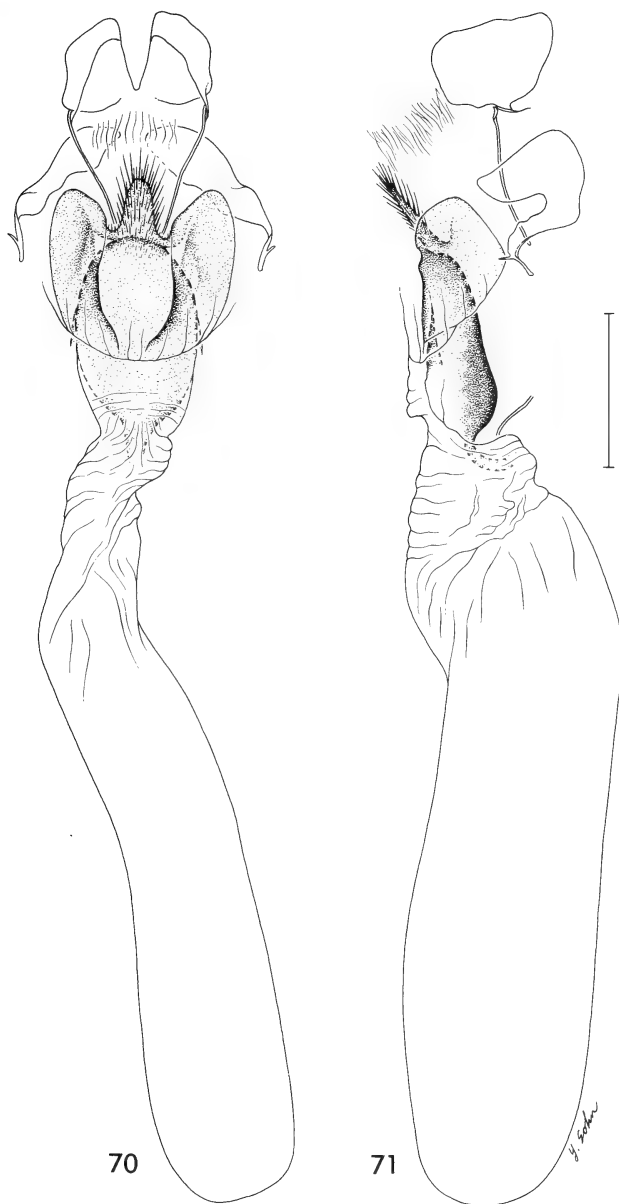
HT♂-IML. Ecuador, Peru, Bolivia, French Guiana, Brazil (Pará, Distrito Federal); Evans (1955) also lists Guyana. 14 ♂ (13 ♂).

See *meridiani*.

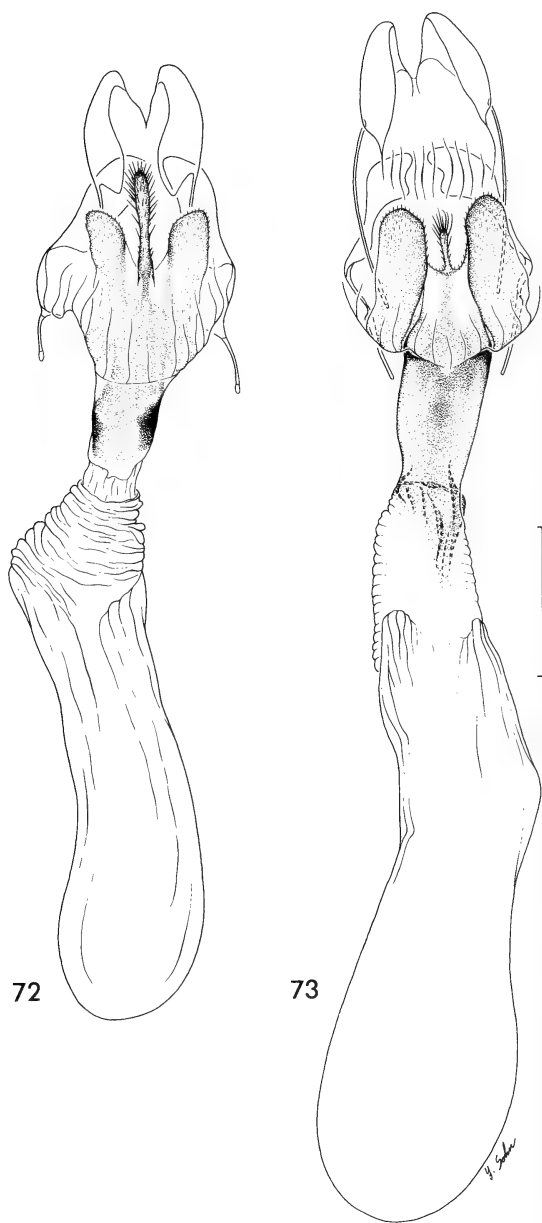
Evans (1955) may have been correct in treating *meridiani* and *pandora* as subspecies. More material is needed to resolve this matter.



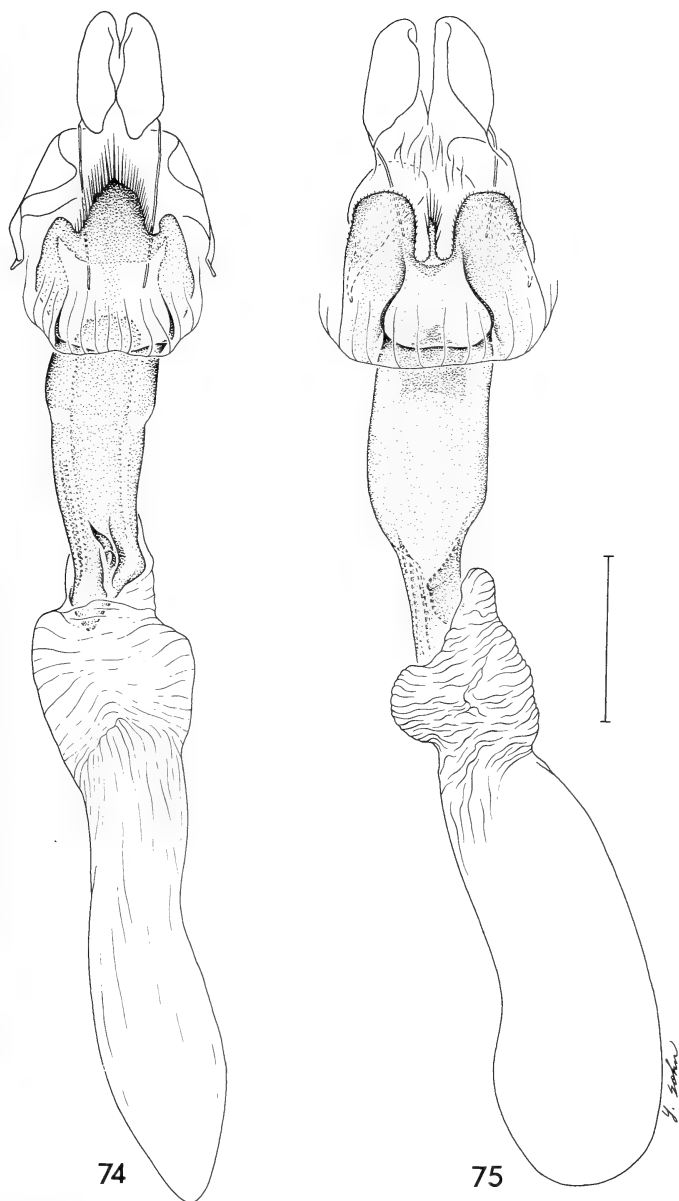
FIGS. 68, 69. Female genitalia of *Quastmellana mexicana* from Rio Metlec, Fortín de las Flores, Veracruz, MEXICO, 2 October 1975, J. Powell and J. Chemsak (X-2809) (UCB). Scale = 1.0 mm. **68**, Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. **69**, The same, plus part of the ductus seminalis, in right lateral view.



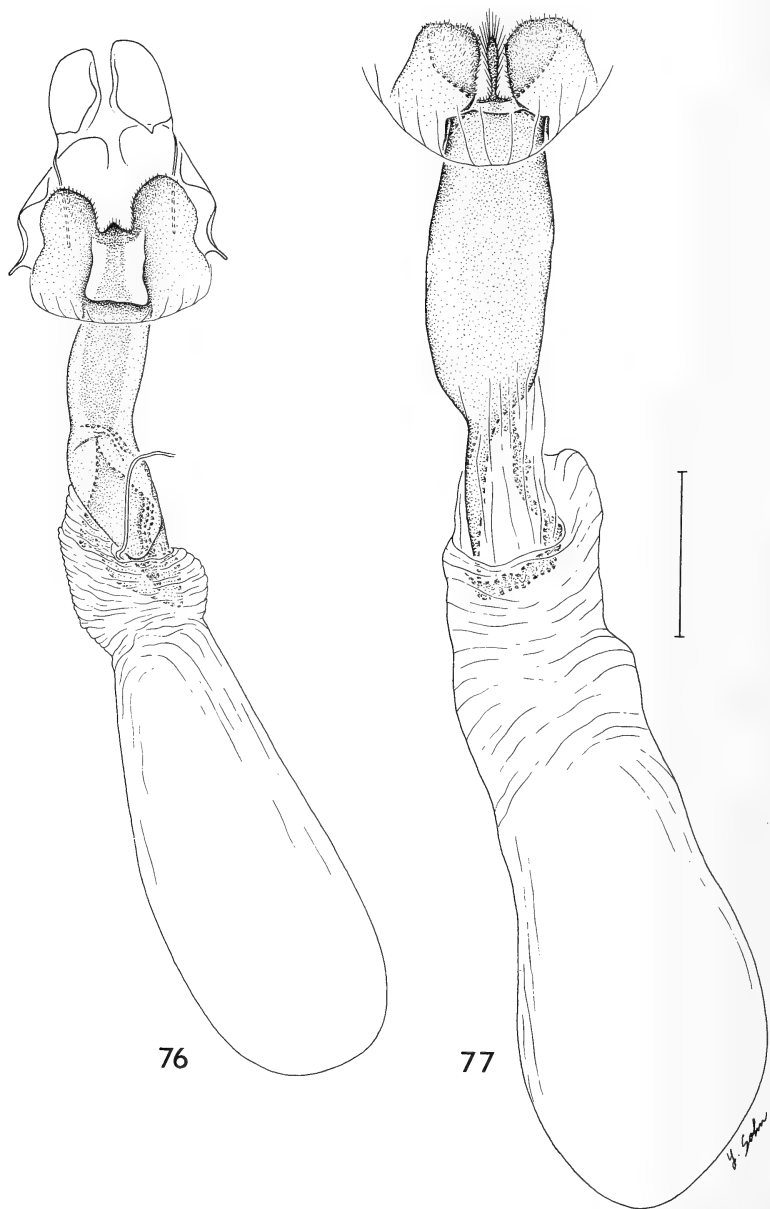
FIGS. 70, 71. Female genitalia of *Quasimellana balsa* from Rte. 16, km 242-254, Sonora, MEXICO, 1 September 1991, J. P. Brock (X-3656) (USNM). Scale = 1.0 mm. **70**, Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. **71**, The same, plus part of the ductus seminalis, in right lateral view.



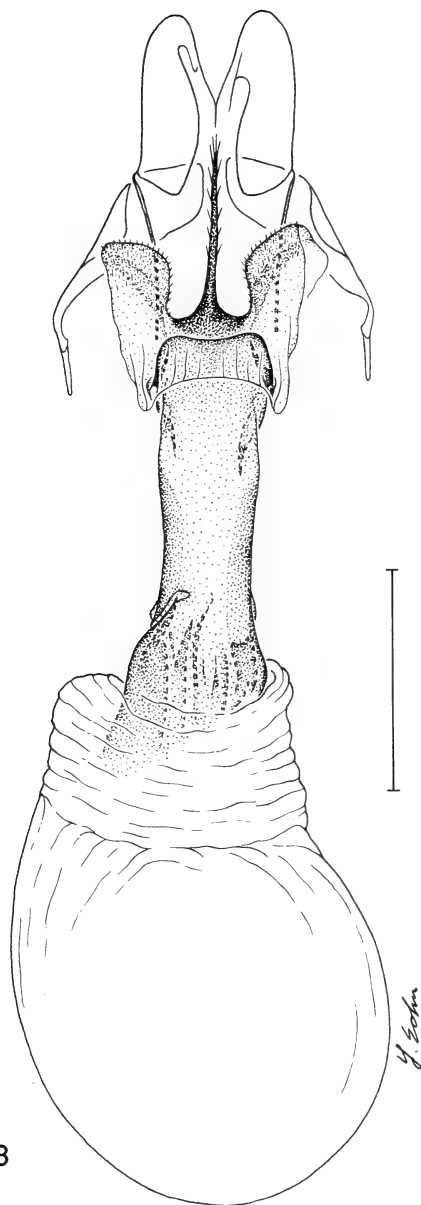
FIGS. 72, 73. Female genitalia of *Quasimellana* showing the sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. Scale = 1.0 mm. **72**, *Q. eulogius* from Cayuga, GUATEMALA, September (X-3062) (USNM). **73**, *Q. mulleri* from Victoria, Tamaulipas, MEXICO, 16 August 1962, Stallings, Turner (X-3648) (AMNH).



FIGS. 74, 75. Female genitalia of *Quasimellana* showing the sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. Scale = 1.0 mm. 74, *Q. aurora* from Las Juntas Verano, 1000 ft (305 m), Hwy. 200 below Puerto Vallarta, Jalisco, MEXICO, 8 August 1989, J. Kemner (X-2823) (USNM). 75, *Q. andersoni* (paratype) from Santa Rosa, Comitán, Chiapas, MEXICO, September 1963, T. Escalante (X-3643) (AMNH).

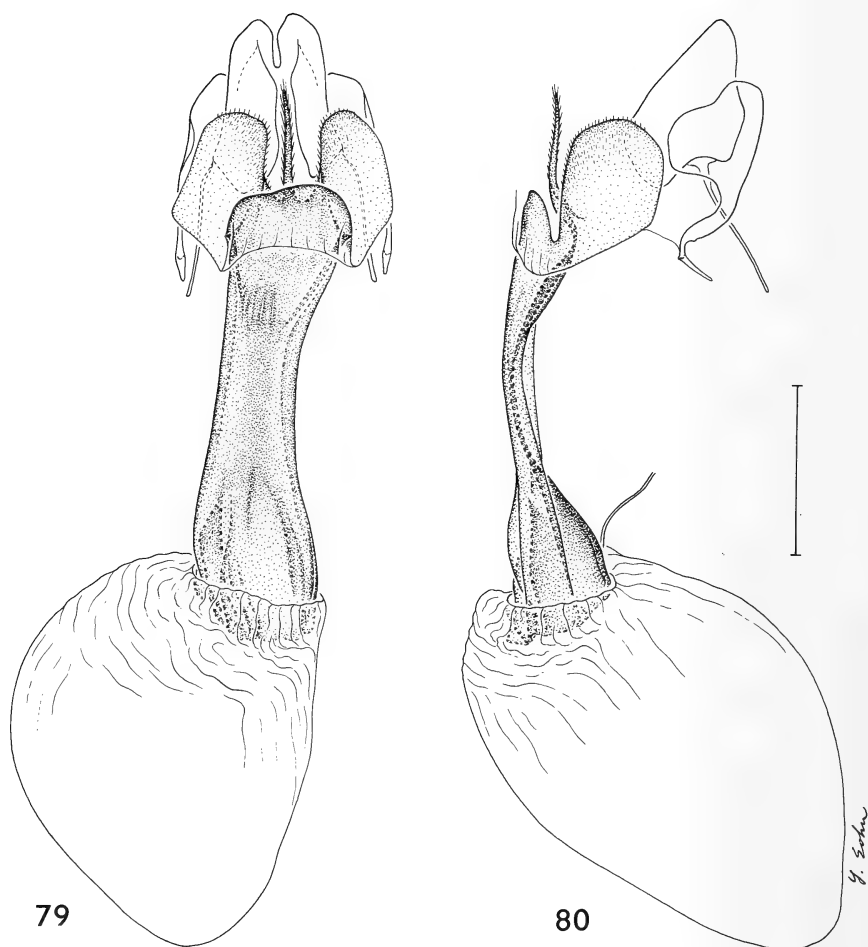


FIGS. 76, 77. Female genitalia of *Quasimellana* showing the sterigma and bursa copulatrix in ventral view. Scale = 1.0 mm. **76**, *Q. sethos*, with an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) and the ductus seminalis, from Howard Air Force Base, Canal Area, PANAMA, 3 February 1985, R. A. Anderson (X-3006) (USNM). **77**, *Q. myron* from Coatepec, Veracruz, MEXICO, (X-2600) (USNM).



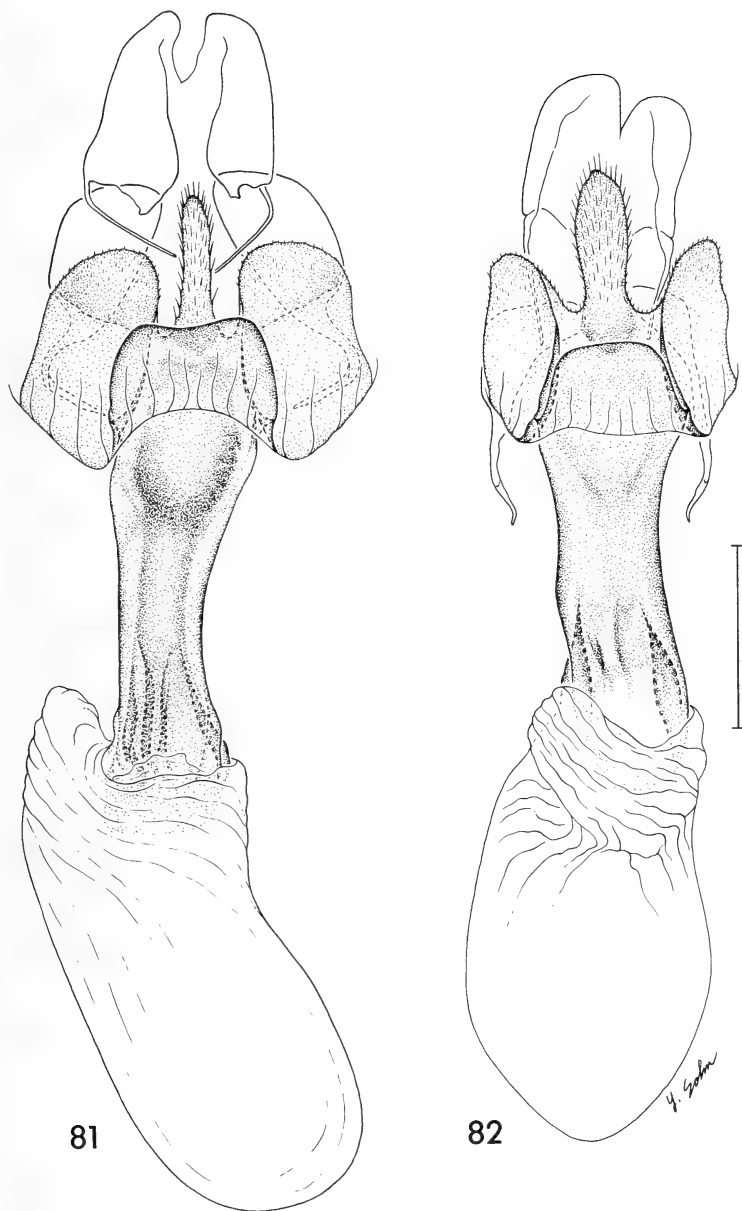
78

FIG. 78. Female genitalia of *Quastmellana amicus* from Napac, 1000 m, Pichincha, ECUADOR, 23 September 1975, S. S. Nicolay (X-2852) (USNM). Scale = 1.0 mm. Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view.

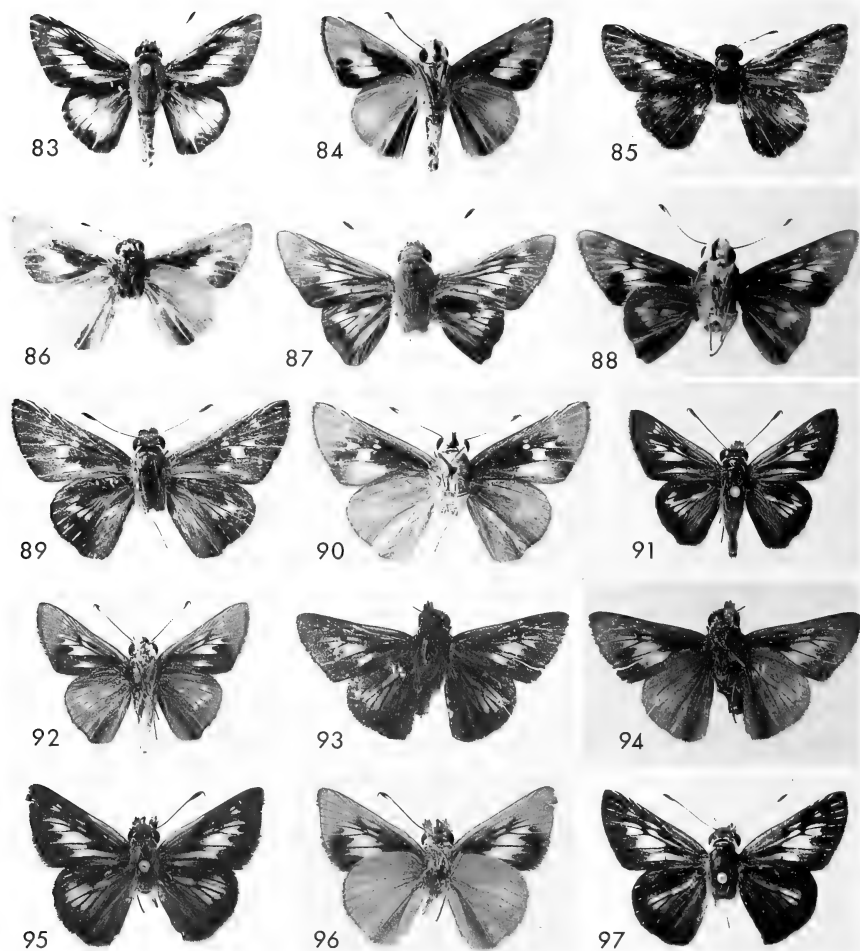


FIGS. 79, 80. Female genitalia of *Quasimellana nicomedes* from Cacatu, Antonina, 20 m, Paraná, BRAZIL, 25 April 1973, Mielke (X-2367) (MacNeill collection). Scale = 1.0 mm. **79**, Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. **80**, The same, plus part of the ductus seminalis, in right lateral view.

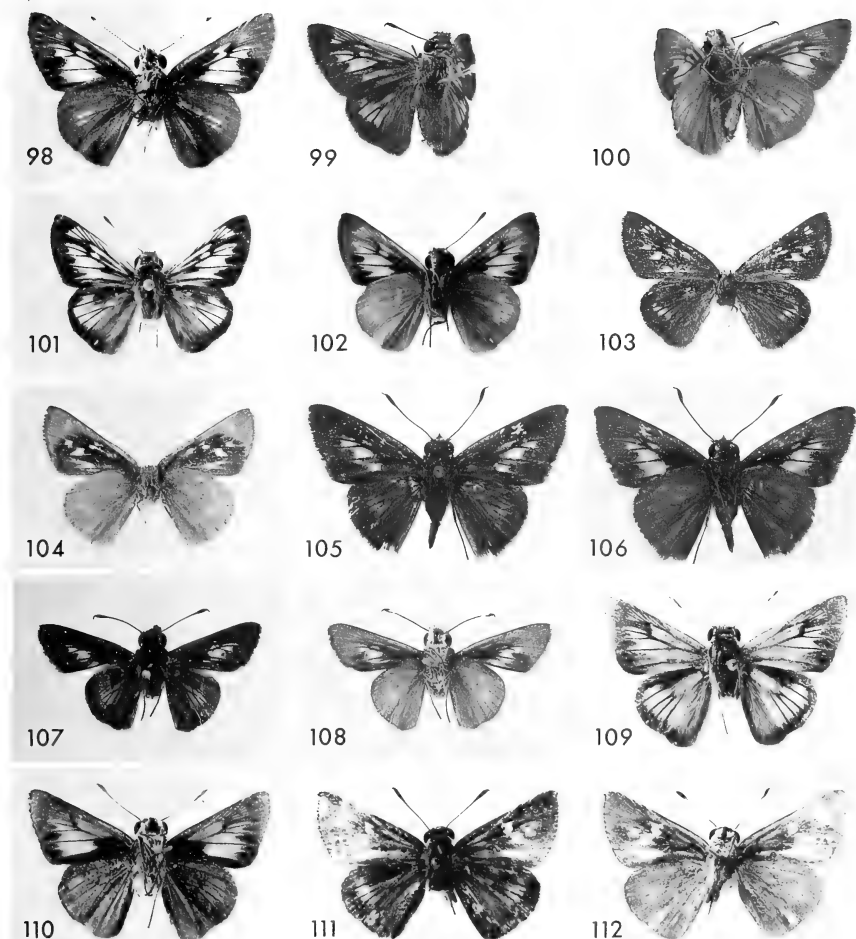




FIGS. 81, 82. Female genitalia of *Quasimellana* showing the sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. Scale = 1.0 mm. **81**, *Q. mielkei* (paratype) from Diamantino, Minas Gerais, BRAZIL, November 1977, Sakakibare (X-3120) (UFPR). **82**, *Q. meridiani* from Dos de Mayo, Misiones, ARGENTINA, 7 March 1989, Foerster (X-3614) (Mielke collection).



FIGS. 83-97. Mostly holotypes (HT) and paratypes (PT) of *Anatrytone* and *Quasimellana* in dorsal (D) and (&) ventral (V) views (all  $\times 1$ ). **83, 84**, *Anatrytone sarah*  $\delta$ , HT, D & V, Limoncocha, 240 m, Napo, ECUADOR (S. S. Nicolay genitalia dissection H739) (USNM). **85, 86**, *A. sarah*  $\varphi$ , PT, D & V, Puerto Maldonado, 290 m, PERU (X-2607) (USNM). **87, 88**, *Quasimellana mexicana*  $\delta$ , HT, D & V, La Gloria, Cardel, Veracruz, MEXICO (W. D. Field genitalia dissection 1820) (USNM). **89, 90**, *Q. mexicana*  $\varphi$ , D & V, Rio Metlec, Fortín de las Flores, Veracruz, MEXICO (X-2809) (UCB). **91, 92**, *Q. siblinga*  $\delta$ , HT, D & V, El Vado-San Sebastian, 1675-1980 m, Oaxaca, MEXICO (USNM). **93, 94**, *Q. noka*  $\delta$ , HT, D & V, locality unknown (X-3457) (BMNH). **95, 96**, *Q. pazina*  $\delta$ , HT, D & V, Yungas and La Paz, 1000 m, BOLIVIA (X-3460) (BMNH). **97**, *Q. antipazina*  $\delta$ , HT, D, La Estrella, 1500 m, Cartago, COSTA RICA (X-2592) (USNM).



FIGS. 98–112. Holotypes (HT) and paratypes (PT) of *Quasimellana* in dorsal (D) and (&) ventral (V) views (all  $\times 1$ ). **98**, *Q. antipazina* ♂, HT, V, La Estrella, 1500 m, Cartago, COSTA RICA (X-2592) (USNM). **99**, **100**, *Q. sista* ♂, HT, D & V, VENEZUELA (X-3459) (BMNH). **101**, **102**, *Q. andersoni* ♂, HT, D & V, Tapalapa, Veracruz, MEXICO (X-3003) (USNM). **103**, **104**, *Q. andersoni* ♀, PT, D & V, Santa Rosa, Comitán, Chiapas, MEXICO (X-3643) (AMNH). **105**, **106**, *Q. verba* ♂, HT, D & V, Balzapamba, Bolívar, ECUADOR (X-3458) (BMNH). **107**, **108**, *Q. angra* ♂, HT, D & V, Pará, BRAZIL (X-3461) (BMNH). **109**, **110**, *Q. mielkei* ♂, HT, D & V, Diamantino, Minas Gerais, BRAZIL (X-3119) (UFPR). **111**, **112**, *Q. mielkei* ♀, PT, D & V, Diamantino, Minas Gerais, BRAZIL (X-3120) (UFPR).

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## IMMATURE STAGES OF VENEZUELAN DIOPTINAE (NOTODONTIDAE) IN *JOSIA* AND *THIRMIDA*

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**ABSTRACT.** Immature stages of five species of Dioptinae (Notodontidae) from Venezuela are described and illustrated. Four are in the genus *Josia* Hübner and one is in *Thirmida* Walker. All feed as larvae on *Passiflora* (Passifloraceae). This is the first life history reported for a member of *Thirmida*. Immature stages are described for each species, and distributional and hostplant data are provided. The tribe Josiini, formerly a subfamily (Josiinae), is delineated. It comprises 103 species in eleven dioptine genera. *Josia turgida* and *Thirmida discinota*, treated by previous authors as subspecies, are revised to species status.

**Additional key words:** Josiini, *Passiflora*, montane forest, larval morphology.

The Neotropical moth subfamily Dioptinae is unique among Notodontidae in containing many diurnal forms with aposematic color patterns (Hering 1925, Köhler 1930, Miller 1992a). The group includes over 400 described species (Byrk 1930), most of which are poorly represented in museums worldwide. The most commonly collected dioptines are those in *Josia*, a genus distributed from southern Mexico south to northern Argentina. *Josia* adults are strikingly colored, usually with orange or yellow markings against a dark ground color, and they tend to fly in a slow, fluttering manner. The caterpillars, which feed on plants in the genus *Passiflora* (Passifloraceae), commonly called “passion flowers,” are conspicuously patterned with various hues of reddish maroon, yellow, and white.

Among Lepidoptera only two large species radiations are associated with *Passiflora*—*Josia* and its relatives, and members of the butterfly subfamily Heliconiinae (Nymphalidae). *Heliconius*, containing approximately 70 Neotropical species (Brown 1981, DeVries 1987), has been the subject of intense ecological and evolutionary research, and an immense amount of biological data has accumulated. For example, there are over 350 published host records for the genus (Benson 1978). In contrast, the amount of biological information available for *Josia* is minute; hosts are recorded for only five species, all from Brazil (Spitz 1931, d’Almeida 1932, Bienzanko 1962a, 1962b, Silva et al. 1968). In this paper we describe the immature stages of five *Passiflora*-feeding Dioptinae from Venezuela.



TABLE 1. Genera belonging in the tribe Josiini (Notodontidae: Dioptinae) based on presence of a kettle-drum metathoracic tympanum in the adult (see text). Generic names follow Watson et al. (1980). Numbers of species for each genus are from Bryk (1930).

Genus	Number of included spp.
<i>Leptactea</i> Prout	1
<i>Mitradaemon</i> Butler	5
<i>Josia</i> Hübner	68
<i>Scea</i> Walker	12
<i>Thirmida</i> Walker	6
<i>Cyanotricha</i> Prout	2
<i>Phavaraea</i> Walker	2
<i>Scedros</i> Walker	1
<i>Getta</i> Walker	3
<i>Anticoreura</i> Prout	1
<i>Polyptychia</i> Felder	2
Total number of species	103

Previous systematic studies have shown that *Josia* belongs in a large, well-defined clade that includes other dioptine genera. Below, we review the evidence supporting that hypothesis.

### The Tribe Josiini

Most notodontid adults have a relatively simple metathoracic tympanum (Surlykke 1984, Scoble 1992) characterized by a shallow dorsal invagination of the epimeron, with the tympanal membrane above, facing postero-ventrally. Richards (1932), in his classic study of noctuid tympanal morphology, described a unique type, which he termed the "kettle-drum" tympanum, found in the dioptine genera *Cyanotricha* and *Josia*. In these genera, the epimeron is greatly invaginated to form a large, enclosed chamber. The tympanal membrane, oriented horizontally, forms the ceiling of the chamber (the "head" of the kettle-drum). The chamber opens to the outside by means of a small lateral hole. The kettle-drum tympanum is figured in Börner (1939: fig. 41), Sick (1940: figs. 1–4), Kiriakoff (1950: figs. 9, 10), and Miller (1991: fig. 240).

After studying tympana throughout the Dioptinae, Sick (1940) created "Group V" for those genera with a kettle-drum tympanum. Group V contained eight genera: *Mitradaemon* Walker, *Josia* Hübner, *Scea* Walker, *Thirmida* Walker, *Cyanotricha* Prout, *Phavaraea* Walker, *Getta* Walker, and *Polyptychia* Felder. Kiriakoff (1950) also noted the highly derived tympanum of *Josia*. He divided the "Dioptidae" into two subfamilies: the Dioptinae with a simple tympanum and the Josiinae with a kettle-drum tympanum. Although Kiriakoff examined fewer



FIG. 1. Map of Venezuela; state boundaries shown with dashed lines (scale bar = 100 km).

taxa than Sick, his list of genera for the Josiinae corresponds closely with Group V. Recent findings have shown that, rather than being a separate family as previous authors had supposed, the Dioptinae is a highly derived subfamily within the Notodontidae (Minet 1983, Weller 1989, Miller 1991, 1992b). Kiriakoff's divisions thus can be recognized as tribes, the Dioptini and Josiini (*new status*).

We performed an exhaustive survey of tympanal structure in the Dioptinae. In addition to the eight genera in Sick's (1940) Group V, we discovered three monobasic genera with the kettle-drum tympanum: *Leptactea* Prout, *Scedros* Walker, and *Anticoreura* Prout. According to our definition, the tribe Josiini includes 103 described species in 11 genera (Table 1).

#### Previous Works on the Josiini

Although early authors did not formally recognize the Josiini, they nevertheless provided relevant taxonomic treatments of the group. The

two most important are Prout's (1918) preliminary revision of dioptine genera and Hering's (1925) contribution to Seitz, where species diagnoses are provided and adults of many taxa are figured. Two keys to *Josia* adults are available, one in Walker (1854: 289-290), and a more complete one in Forbes (1931). Forbes (1939) also gave keys and diagnoses for five josiines from Barro Colorado Island, Panama.

Morphological and biological data are scant. Markin et al. (1989) described the biology and life stages of *Cyanotricha necyria* Felder, a josiine species from the western Andes. Miller (1988) described the genitalia and copulatory mechanism of *C. necyria*, and also has discussed various features of josiine larval and adult morphology within the context of a reclassification of the Notodontidae (Miller 1991). Papers by other authors give only anecdotal information on immatures. Because of the paucity of published work on the Josiini, we have chosen to present considerable detail in this paper.

## METHODS

During the course of our research we visited sites in mountain systems of the Cordillera de la Costa in the state of Aragua of northern Venezuela, and in the Cordillera de Mérida in western Venezuela, specifically in the states of Mérida and Barinas (Fig. 1). Our collecting covered a range of elevations (540 to 2420 m), life zones, and vegetation types. We use Holdridge's life zone system, relying on the work of Ewel et al. (1976) to identify life zones for each of our collecting sites. Life zone types are indicated by an abbreviation in parentheses after the locality. The altitudes provided are plus or minus 50 m.

Most of our collecting sites showed varying degrees of habitat disturbance, usually due to agriculture. Large tracts of land in the Cordillera de Mérida and Cordillera de la Costa have a long history of agricultural use, and the vegetation currently present, even in some forested sites, may be secondary. Primary vegetation is often reduced to relictual patches or is limited to steep mountain slopes. Four of our collecting sites are within the limits of national parks, Parque Nacional Henri Pittier in the state of Aragua, and Sierra Nevada in Mérida. In these officially protected areas, the vegetation is likely to be primary.

*Passiflora* leaves with eggs or larvae of Josiini were picked in the field and transported to the laboratory inside moistened plastic containers. In the lab, leaves were transferred into small glass flasks containing water, submersing the petiole, and plugging the neck of the flask around the petiole with wet paper. Each flask was placed in a plastic dish and covered with an inverted 1 liter transparent plastic container. Leaves usually remained fresh in the rearing containers for

several days. Fresh food was provided when leaves were consumed or showed signs of deterioration.

For two of the species, *Josia radians* and *J. aurifusa*, adult females were collected in the field, placed in plastic bags with host foliage, and brought to the lab. Females laid eggs on the enclosed leaves over a period of two to three days.

Larvae were fed leaves of the *Passiflora* upon which they were discovered in the field, or on an alternative species when the original host was not easily available. Certain of the josiines lay eggs in batches. For these, egg masses were divided and reared in more than one container. Frass accumulations were discarded regularly. Instar durations were not monitored precisely; we therefore give only the approximate development time from field-collected egg to adult emergence. At least for the first, second, and third instars, each stadium lasts approximately five or six days.

We preserved specimens of eggs, first and last instar larvae, and adults. Larvae were preserved by dropping them into hot water (just below boiling temperature) for several seconds, and then transferring them to vials of 70% ethanol. Shed head capsules were saved in alcohol along with the associated specimens. Pupal exuviae were mounted on the same pin as the adult voucher. Voucher material is deposited in the collections of the Museo del Instituto de Zoología Agrícola, Maracay (MIZA) and the American Museum of Natural History, New York (AMNH).

Identifications of adult moths were confirmed by comparison with type specimens. Comparisons between genitalic dissections of vouchers and types were required for *Josia radians*, *J. aurifusa*, and *J. turgida*. These three belong to difficult species complexes, the resolution of which will require study of large series from a wide range of localities. This was beyond the scope of the present work.

The Passifloraceae contains twenty genera and approximately 600 species (Heywood 1979). Over 400 species are placed in the genus *Passiflora*, with all but 20 occurring in the Neotropics (Holm-Nielsen et al. 1988, Gentry 1993). Stephan S. Tillet (Herbario Ovalles, Facultad de Farmacia, Universidad Central de Venezuela, Caracas) verified host-plant identifications. We assign *Passiflora* species to subgenera following Killip (1938), who recognized 22 subgenera for the American flora. However, the classification of *Passiflora* currently is undergoing revision (J. MacDougal and C. Feuillet, pers. comm.), so these assignments are provisional. Plant distributions are based on Killip (1938) and Holm-Nielsen et al. (1988).

Nomenclature for larval morphology follows Stehr (1987) and Pe-

terson (1962). We employ the system for larval chaetotaxy developed by Hinton (1946), but have incorporated minor modifications suggested in Miller (1991) and Rawlins (1992). For first instars we use the setal nomenclature of Kitching (1984) on Danaini (Nymphalidae) and Fleming (1960) on Heliconiinae. Pupal terminology follows Mosher (1916). Larval measurements were made using a Microcode II (Boeckeler Instruments) digital micrometer attached to a Zeiss SV8 stereomicroscope. Electron micrographs were taken with a Zeiss DSM 950 Digital Scanning Microscope.

**Abbreviations.** A = abdominal segment; CuA = cubital wing vein; D = dorsal seta; DC = discal cell; FW = forewing; HW = hindwing; JSM = James S. Miller; L = lateral seta; LDO = L. Daniel Otero; LM-mf = lower montane moist forest; LM-wf = lower montane wet forest; M = medial wing vein; P = posterior seta; PM-df = premontane dry forest; PM-mf = premontane moist forest; PM-wf = premontane wet forest; R = radial wing vein; SD = subdorsal seta; SV = subventral seta; T1 = prothoracic segment; T2 = mesothoracic segment; T3 = metathoracic segment; T-mf = tropical moist forest; TS = tarsal seta; V = ventral seta. (Additional abbreviations are given in the figure legends.)

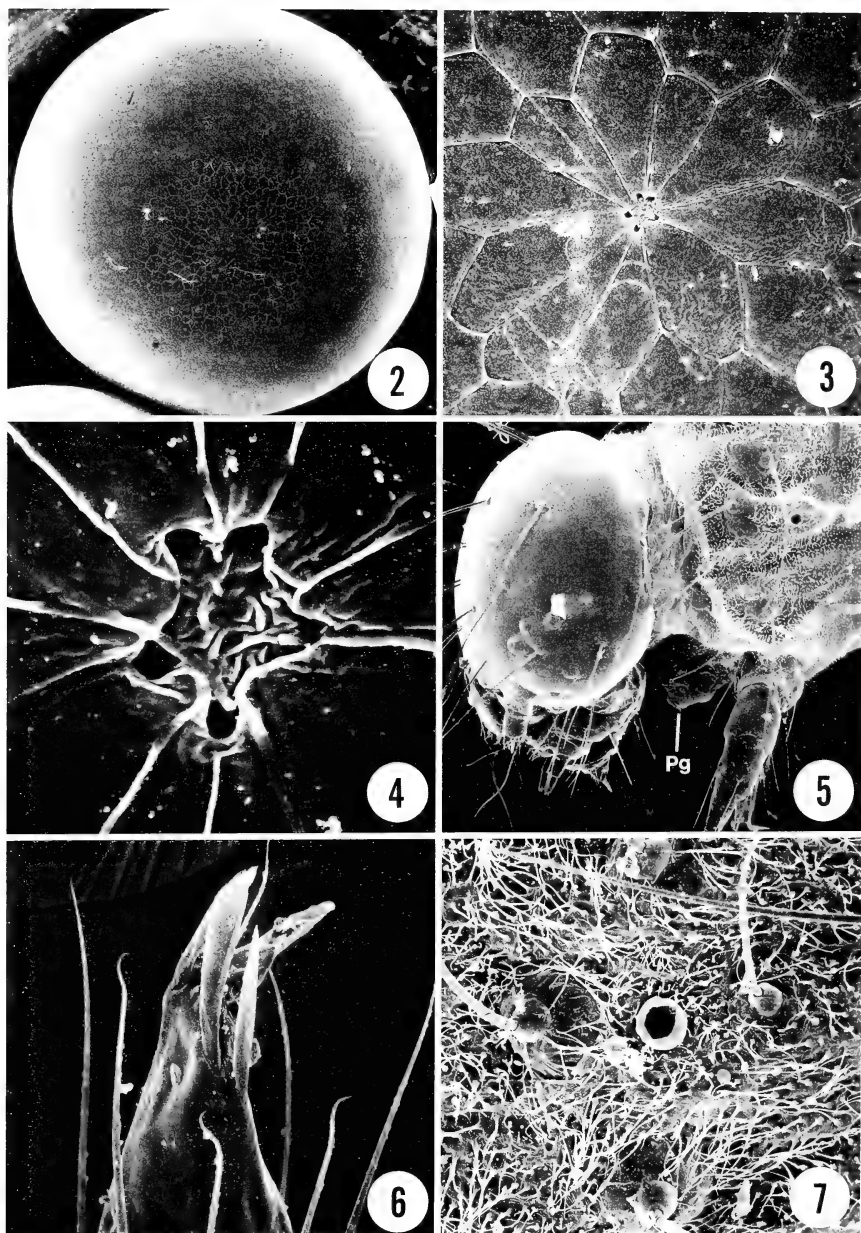
**Acronyms for Museums.** AMNH = American Museum of Natural History, New York, NY; BMNH = The Natural History Museum, London, Great Britain; CMNH = Carnegie Museum of Natural History, Pittsburgh, PA; CUIC = Cornell University Insect Collections, Ithaca, NY; LACM = Los Angeles County Museum of Natural History, CA; MIZA = Museo del Instituto de Zoología Agrícola, Maracay, Venezuela; MNHN = Muséum National d'Histoire Naturelle, Paris, France; NMNH = National Museum of Natural History, Washington, DC; ZMH = Zoologisches Museum, Humboldt-Universität, Berlin, Germany.

## GENERAL ACCOUNT

Many of the traits we observed are found throughout our study taxa. General morphological features, as well as those that provide potentially useful taxonomic differences, are summarized below.

**Egg.** The pearly white eggs are almost perfectly spherical (Figs. 2, 15), without surface sculpturing except for a fine reticulate pattern in the area surrounding the micropyle (Figs. 3, 4). Among the five study species, egg size ranges from 0.70 to 1.10 mm in diameter. They are laid either individually, or in small clusters of up to 25 eggs (Fig. 15).

**First Instar Larva.** All first instars in this study exhibit the same simple primary setal pattern (Figs. 47, 56, 71, 78); setae L2 and L3 absent on segments T2 and T3, L3 absent on A1–A7. This configuration also occurs in first instars of Nymphalidae (Kitching 1984), Heliconiinae (Fleming 1960), and Noctuidae (Merzheevskaya 1988), and is probably



FIGS. 2-7. Scanning electron micrographs of *Thirmida discinota* immature stages. 2, Egg, dorsal view ( $\times 79$ ); 3, Micropyle and surrounding area ( $\times 1263$ ); 4, Micropyle ( $\times 6960$ ); 5, Head and T1 of first instar, lateral view ( $\times 97$ ); 6, Tarsus of first instar T3 leg, mesal view ( $\times 596$ ); 7, A8 spiracle and setal bases, first instar ( $\times 344$ ). [Pg = prothoracic gland.]

distributed throughout the Lepidoptera. Features restricted to first instar larvae include: antenna short (Figs. 5, 48, 61, 79); spinneret long and apically acute (Figs. 5, 48, 61, 79); mandible serrate (Godfrey et al. 1989); tarsal setae elongate (Figs. 6, 49); each primary seta located on a prominent, sclerotized pinaculum (Figs. 5, 7, 47, 56, 71, 78); spiracles extremely small, round (Figs. 5, 7); color pattern simple, either entirely white or with alternating reddish bands (compare Figs. 47 and 56).

**Fourth (Final) Instar Larva.** Subprimary setae are defined as those that appear after the first larval molt (Hinton 1946, Kitching 1984). In the josiines we studied, second, third, and fourth instars have the same setal pattern. However, patterns can vary between species, suggesting that subprimary setae may be useful in josiine systematics. For example, fourth instars of *Josia gopala* possess an L seta on segments A2–A6 not found in other species (compare Figs. 52 and 67). In *Thirmida discinota*, L3 on A3–A6 is multiple, and there are novel setae on the anal plate (Figs. 43, 44). Characters such as these may provide useful synapomorphies for defining subclades within the Josiini. Color pattern differences provide important characters for separating species.

A diagnosis of last instar larval morphology for Josiini is as follows: Head either entirely black (Fig. 45), or white with dark dorso-ventral stripes (Figs. 54, 69, 76, 85); mandibular margin smooth (Godfrey et al. 1989); antenna with segment 2 longer than segment 1, segment 3 short (Figs. 10, 51, 80, 81); spinneret short and wide (Figs. 11, 50, 62). Primary setal pattern generally as in other Notodontidae; secondary setae occasionally present on head and body (in *Cyanotricha necyria*; Miller 1991); tarsal setae TS2 and TS4 lanceolate with apices acute, TS3 broad, leaf-shaped (Figs. 12, 13, 57, 63, 82); prothoracic gland present (Figs. 8, 9, 43, 52, 67, 74, 83); thorax and abdomen lacking projections, but with a slight hump on A8 (Figs. 44, 53, 68, 75, 84); cuticle glossy in appearance, covered with microprojections (=“shagreened;” e.g., Figs. 5, 7, 20–23); body variously patterned with reddish maroon, yellow and white (Figs. 14–19); A8 spiracle either subcircular or an elongate oval (Figs. 21–23); terminal segments often conspicuous, white (Figs. 16–19); prolegs on A10 reduced but functional (Figs. 44, 53, 68, 75, 84); segments A7–A10 frequently held aloft (Figs. 16, 18, 19); like other Dioptinae (but unlike other Notodontidae), a single MD seta on A1 rather than two (Miller 1991).

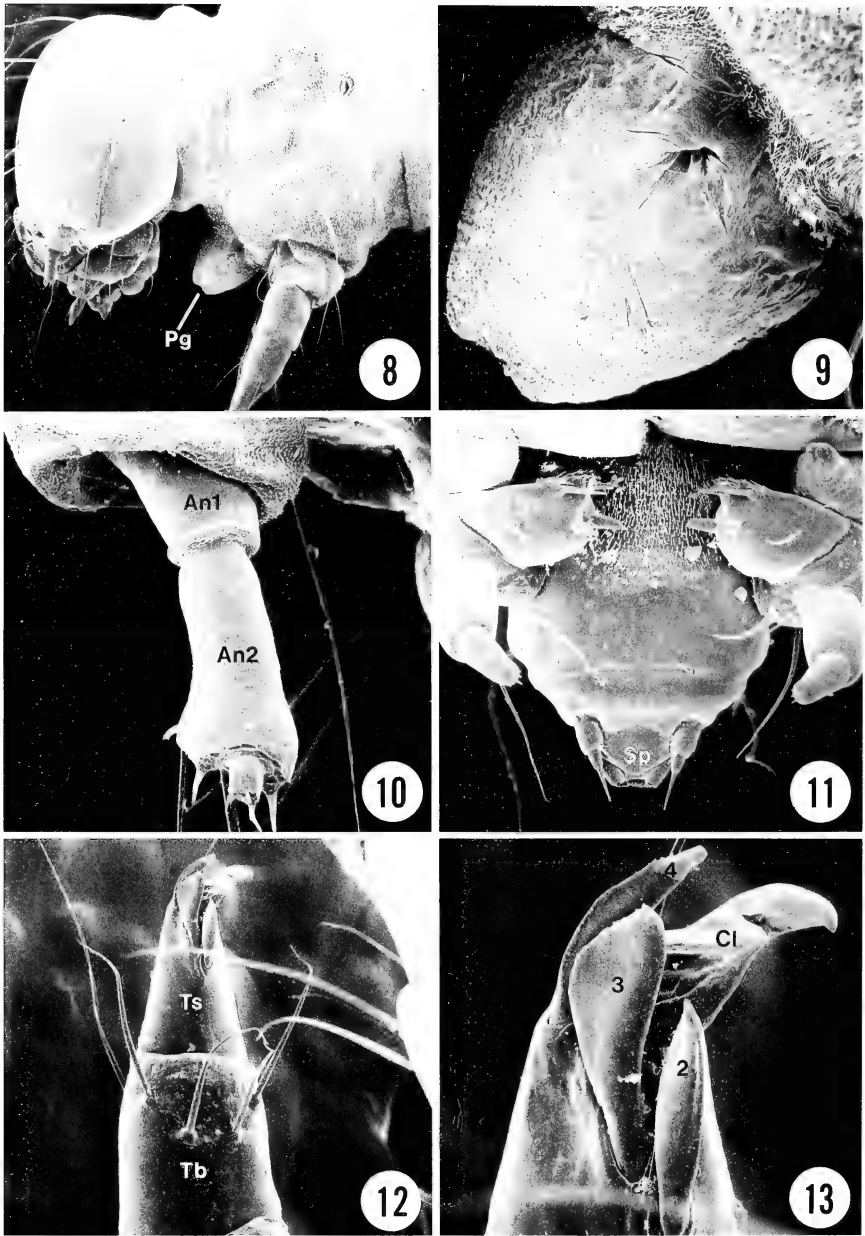
**Pupa.** Most features of josiine pupal morphology do not show significant variation (see Miller 1992b: figs. 31, 32). However, the cremaster varies in shape, and in the number and size of the cremaster setae (Figs. 24, 25, 58–60, 64–66).

**Adult.** Many external adult traits show variation, and these can be used in identification. Examples include the shape of the labial palpus and length of the pectinations on the male antenna. The forewing can exhibit a longitudinal stripe (Figs. 28–36), a transverse one (Hering 1925), or variations on the latter (Figs. 26, 27). The species of Josiini also differ greatly in size; FW lengths range from 11 mm (*Josia ena* Boisduval) to 28 mm (*Phavaraea rejecta* Hübner).

## SPECIES ACCOUNTS

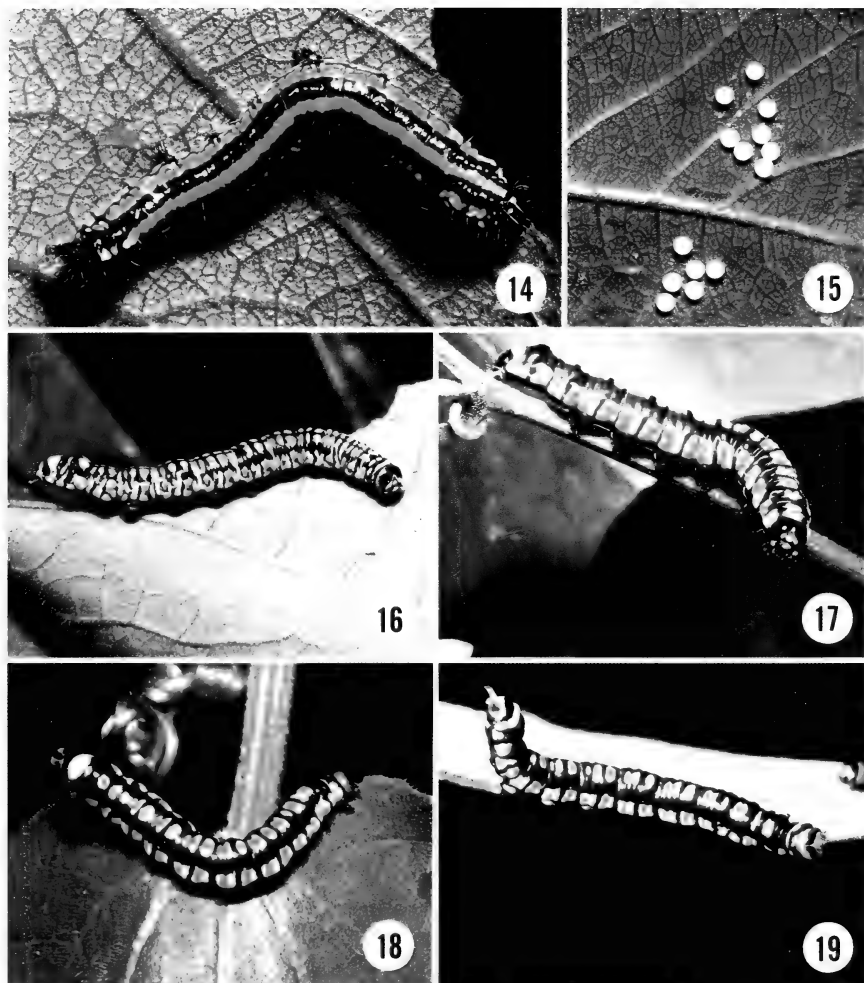
### *Thirmida discinota* Warren, 1900, revised status

**Distribution.** This species is known almost exclusively from localities close to the city of Mérida. However, a single specimen (MIZA) from the State of Lara has the following data: Parque Nacional Yacambú, El Blanquito, 1350 m; 1–3/VIII/1976; C. J. Rosales, L. J. Joly. This is the lowest elevation from which *T. discinota* is known; all the other specimens were collected at or above 2000 m. Data for the female holotype (BMNH) is given as Pedregosa, Mérida, 3000 m, October 1897 (Briceño) (Warren 1900:129), a locality southwest of the city of Mérida. *Thirmida discinota* is rare in collections. Previously it was represented



FIGS. 8-13. Scanning electron micrographs of fourth instar *Thirmida discinota* larva. **8**, Head and T1 ( $\times 22$ ); **9**, Prothoracic gland, lateral view ( $\times 133$ ); **10**, Antenna, frontal view ( $\times 180$ ); **11**, Maxillary and hypopharyngeal complexes, frontal view ( $\times 133$ ); **12**, Tibia and tarsus of right T2 leg, mesal view ( $\times 82$ ); **13**, Tarsus of right T2 leg, mesal view ( $\times 290$ ). [An = antennal segment; Cl = tarsal claw; Pg = prothoracic gland; Sp = spinneret; 2, 3, 4 = tarsal setae 2, 3, and 4.]

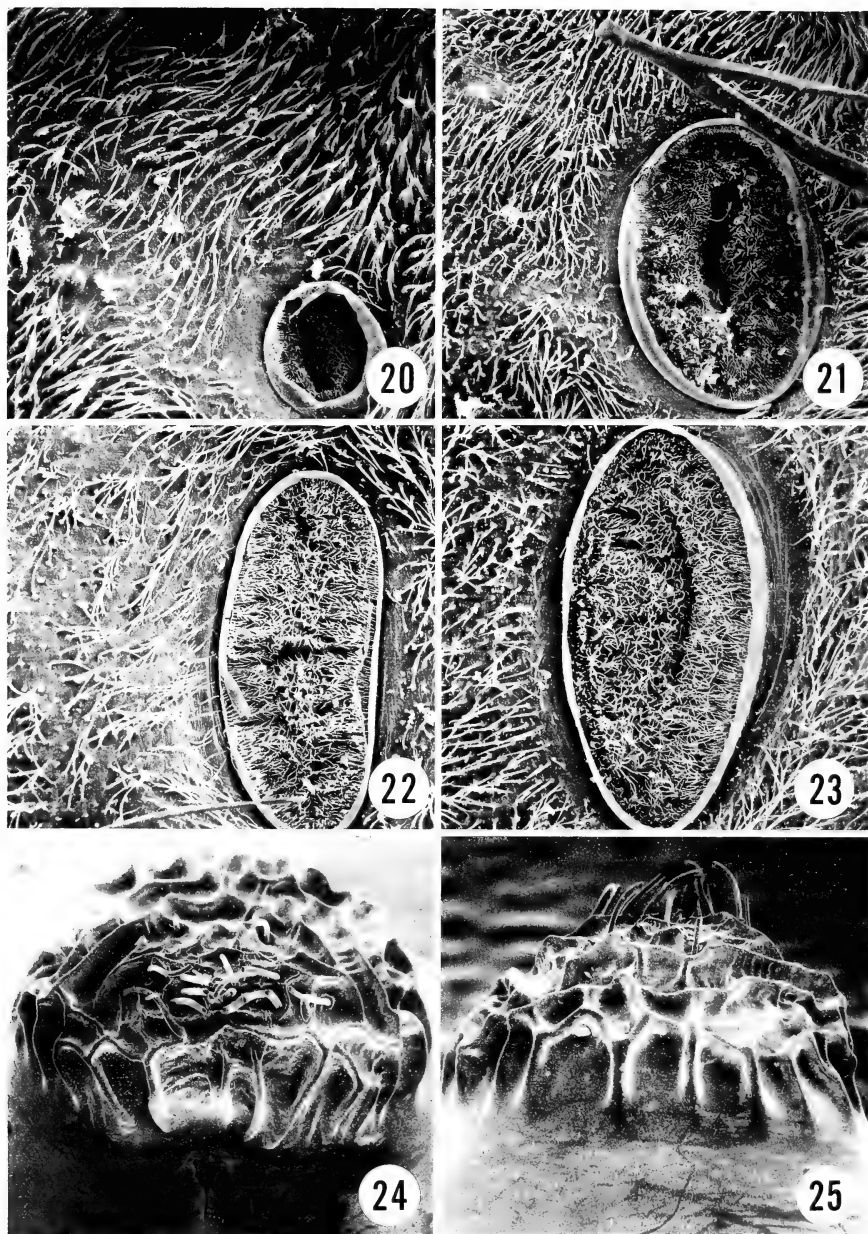




FIGS. 14-19. Immature stages of Josiini. 14, Fourth instar larva of *Thirmida discinota* on *Passiflora bauhinifolia*; 15, Eggs of *Thirmida discinota* laid on the underside of *P. bauhinifolia* leaves; 16, Fourth instar of *Josia radians* on *Passiflora capsularis*; 17, Fourth instar larva of *Josia gopala* on *Passiflora cuneata*; 18, Fourth instar larva of *Josia aurifusa* on *P. capsularis*; 19, Fourth instar larva of *Josia turgida* on *P. capsularis*. Photographs by L. Daniel Otero.

in major museums by a total of 13 specimens (BMNH, MIZA, NMNH, and ZMH), most of which were collected near the turn of the century. We have found it to be locally abundant.

**Collecting Localities.** Recorded from Quebrada La Caña on the road from El Valle to La Culata, northwest of Mérida, at 2420 m (31 October



FIGS. 20-25. Scanning electron micrographs of Josiini immature stages. 20, A4 spiracle, fourth instar *Thirmida discinota* larva (note seta MSD2 at left) ( $\times 211$ ); 21, A8 spiracle, fourth instar *T. discinota* larva ( $\times 151$ ); 22, A8 spiracle, fourth instar *Josia aurifusa* larva ( $\times 248$ ); 23, A8 spiracle, fourth instar *Josia radians* larva ( $\times 243$ ); 24, Cremaster of *T. discinota* pupa, postero-ventral view ( $\times 58$ ); 25, Cremaster of *T. discinota*, dorsal view ( $\times 59$ ).

1992, 17 January 1993, and 6 April 1993). The life zone for this locality is regarded as lower montane moist forest (LM-mf) according to Ewel et al. (1976). However, only relictual patches of the original forest type remain, and the habitat where we found *T. discinota* is characterized by secondary vegetation that includes shrubs and some small trees (Fig. 42).

**Foodplant.** Eggs of *T. discinota* were collected on vines of *Passiflora bahuinifolia* Kunth (subgenus *Plectostemma*), growing near a stream. There is some confusion regarding the distribution and taxonomic status of this species; Holm-Nielsen et al. (1988) regard it as a synonym of *P. alnifolia* Kunth, and according to Killip (1938) the plant occurs only in southwestern Colombia, Ecuador, and northern Peru.

**Egg.** Relatively large (1.1 mm;  $n = 5$ ); deposited in clusters of 4 to 25 eggs (Fig. 15). Eggs tend to be laid on older leaves than in the other *Josiini* that we observed. Markin et al. (1989) noted a similar preference for mature foliage by ovipositing females of *Cyanotricha necyria* Felder (*Josiini*). Based on field collections, duration of the egg stage is at least 10 days. Development time from field-collected egg to adult = 60–65 days.

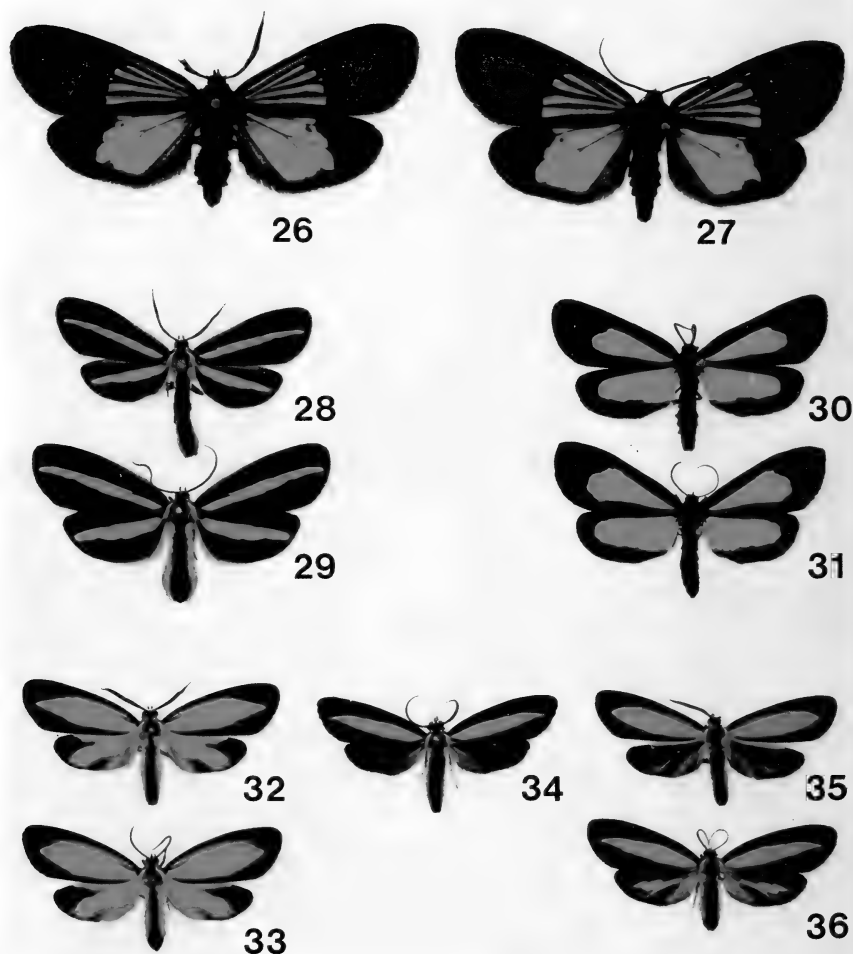
**First Instar.** Head entirely black except for white clypeus; thorax and abdomen unpigmented. Primary setae (Fig. 47) as in general account (above), similar to *Josta*. Body length = 5.24–5.58 mm; head width = 0.77–0.78 mm ( $n = 5$ ).

**Second and Third Instars.** Similar in setal and pigment patterns to final instar larvae. Head widths: 2nd instar = 1.14–1.22 mm; 3rd instar = 1.80–1.88 mm ( $n = 5$ ).

**Final (Fourth) Instar.** Head entirely shiny black except for white clypeus and thin white lines along ecdysial suture and ecdysial lines (Fig. 45); labrum with a whitish central area; antenna with segment 2 expanded distally, approximately twice the length of segment 1. Prothoracic shield (Fig. 46) broad, heavily sclerotized, with a partial medial seam, anterolateral angles not produced; ground color of thorax and abdomen reddish purple (Fig. 14); a lemon yellow longitudinal stripe along dorsal midline bordered on each side by a thin, irregular whitish subdorsal stripe; lateral pattern complex (Figs. 43, 44), composed of a wide yellow longitudinal stripe with reddish purple blotches and an irregular reddish purple stripe within it; venter entirely lemon yellow; segment A9 not conspicuous, mostly maroon above. Tarsal setae with TS2 and TS4 lanceolate, TS3 broad and leaf-shaped, apex emarginate (Fig. 13). Setal pattern (Figs. 43, 44) on thorax and abdomen similar to other *Josiini*, but with the following exceptions: seta SV2 on segment A2 located between L3 and SV3, on a horizontal line with them; one or two additional setae present on proleg-bearing segments (A3–A6) in the L3 position; anal plate with 2–3 additional setae on each side; lateral plate of A10 proleg base with more than 12 setae; all primary setae wide, white and “fleshy” in appearance; each thoracic and abdominal seta on a small, heavily sclerotized pinaculum. Body length = 38.0–39.0 mm; head width = 2.60–2.83 mm ( $n = 5$ ).

**Pupa.** Cremaster (Figs. 24, 25) short and broad, heavily rugose dorsally with broad, longitudinal flutes ventrally; approximately 20 short, hook-shaped setae. Duration: approximately 20 days.

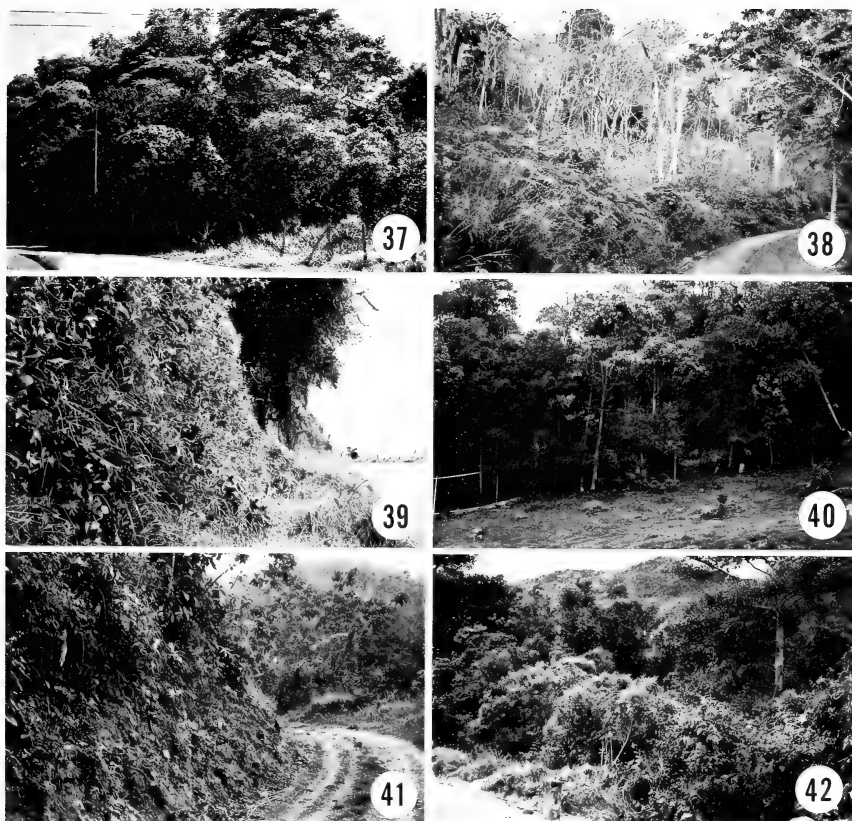
**Adult.** FW length = 23–25 mm. Head, thorax and abdomen gray-brown, abdomen with scattered iridescent bluish scales; pectinations of male antenna long; eye relatively small; front and labial palpus rough-scaled; palpus porrect, narrow, fringed below with long scales; pectus and femur with long, hairlike scales. FW light orange from base to distal end of DC, charcoal gray beyond (Figs. 26, 27); orange region with diffuse, black longitudinal lines along veins, surrounded on anterior, posterior, and distal margins by a black border; HW (Figs. 26, 27) with a light orange central region extending from base to slightly beyond DC, iridescent purple-black merging to charcoal gray beyond; cubital



FIGS. 26-36. Adults of Josiini (life size). 26, *Thirmida discinota*, male; 27, *T. discinota*, female; 28, *Josia radians*, male; 29, *J. radians*, female; 30, *Josia gopala*, male; 31, *J. gopala*, female; 32, *Josia turgida*, male; 33, *J. turgida*, female; 34, *Josia aurifusa*, male (dark form from Puente Victoria); 35, *J. aurifusa*, male; 36, *J. aurifusa*, female. Photograph by Cal Snyder.

vein thinly lined with black scales; a small, black spot on upper discocellular cross vein. Upper and lower wing surfaces the same, except veins below uniformly orange rather than black.

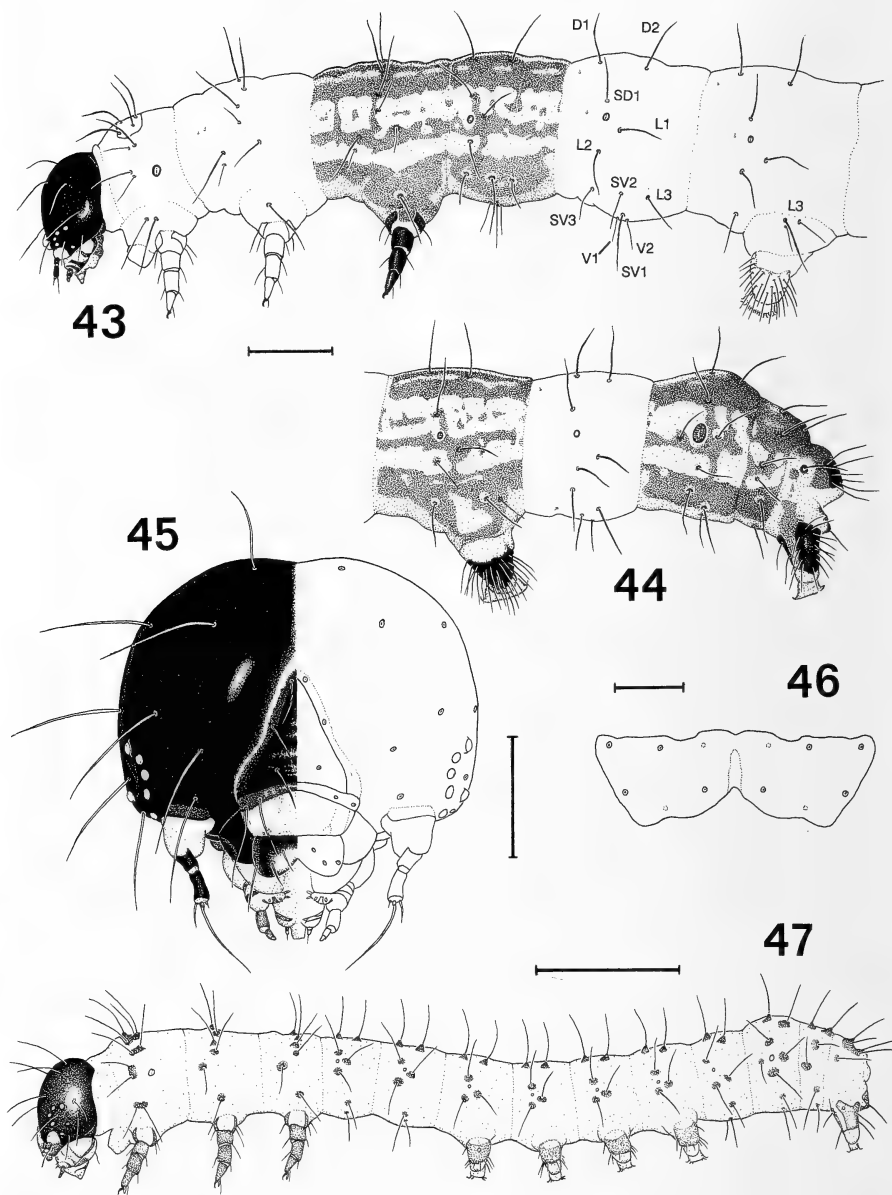
**Discussion.** Warren (1900) described *discinota* in the genus *Scea*, which was at that time placed in the Cylopodinae (Geometridae). His description was based on a single female specimen (BMNH). Warren's taxon was transferred to *Thirmida* in the Dioptinae by Prout (1918),



FIGS. 37–42. Collecting sites for *Josiini* (all in the State of Mérida, Venezuela). **37**, Paseo Los Pinos (1450 m), a locality for *Josia radians*; **38**, Along the road from Estanques to Páramo Las Coloradas (1150 m), a locality for *J. radians*; **39**, Las Playitas, near Bailadores (2250 m), a locality for *J. radians* (the foliage and flowers at left are those of *Passiflora manicata*); **40**, Cloud forest margin (2300 m) in Monterrey, a locality for *J. gopala*; **41**, Puente Victoria (540 m), a locality for *J. aurifusa*; **42**, La Caña on the road from El Valle to La Culata (2420 m), northwest of the city of Mérida, a locality for *Thirmida discinota*. Photographs by L. Daniel Otero.

who considered *discinota* to be a subspecies of *T. dimidiata* Walker. This arrangement was followed by all subsequent authors (Hering 1925, Talbot 1929, Bryk 1930). We compared specimens of *T. dimidiata* from Bogotá, Colombia, the type locality (Walker 1854:466), with our Mérida material, and discovered numerous differences in wing pattern and genitalia. We therefore recognize the two as distinct, hereby returning *Thirmida discinota* to species level status.

Thus we recognize six species in *Thirmida*, five of which are figured in Hering (1925: plate 71). The only one with which *T. discinota* could be confused is *T. dimidiata*. Adults may be separated on the basis of



FIGS. 43-47. Larval stages of *Thirmida discinota*. **43**, Head, thorax, and segments A1-A3 of fourth instar, lateral view; **44**, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); **45**, Head of fourth instar, frontal view (scale line = 1 mm); **46**, Prothoracic shield of fourth instar, dorsal view (scale line = 1 mm); **47**, First instar, lateral view (scale line = 1 mm). [See Figs. 52-56 for key to symbols.]

wing pattern: the orange in the forewing of *T. dimidiata* extends beyond the distal margin of the discal cell, while in *T. discinota* it stops at the end of the discal cell (Figs. 26, 27).

This life history description is the first for a member of *Thirmida*. Adults and immatures of the other species, known from the Andes of Colombia and Ecuador at elevations between 1200 and 2300 m, will likely be discovered by collecting in habitats similar to that of *T. discinota*. Hering (1925), noting wing pattern similarities, suggested that the closest relatives of *Thirmida* are the Andean genera *Scea* and *Cyanotricha*.

Mimicry occurs throughout the Dioprinae (Seitz 1925, Köhler 1930). In his description of the new genus and species *Thermidarctia thermidoides* in the Pericopinae (Arctiidae), Talbot (1929) noted what he called an "almost perfect resemblance" (p. 133) between his taxon and *Thirmida discinota*. Mérida is the type locality for both moths.

*Josia radians* Warren, 1905a

**Distribution.** Bryk (1930) reported *J. radians* from Mexico to Colombia, Guyana, and Venezuela, presumably based on museum specimens. However, *J. radians* frequently is confused with *J. ligata* Walker (type locality Bogotá, Colombia) and *J. frigida* Druce (type locality Las Mercedes, Guatemala). In all probability, the majority of material that Bryk examined was misidentified.

Reliably determined museum material, and specimens we have collected, suggest that the species occurs from the State of Aragua, Venezuela west to the Colombian border. It probably occurs in eastern Colombia as well. Although there is no locality data on the holotype, Warren's (1905a) description of *J. radians* gave the following: "1 male from Onaca, Sta. Martha, 2200 ft., wet season, September-October 1901 (Engelke)." We have been unable to locate this site, but assume that it is a misspelling of Ocaña, a locality in the eastern Cordillera of Colombia near the Venezuelan border (Fig. 1).

**Collecting Localities.** Eggs, larvae, and adults of *Josia radians* were collected at eight different localities (Figs. 37-39, 72). There were seven sites in the state of Mérida, and an eighth locality in the Parque Nacional Henri Pittier, State of Aragua. Elevations ranged from 1100 m (near El Amparo) to 2250 m (Las Playitas, near Bailadores). These collecting sites cover a variety of life zones (PM-mf, PM-wf, PM-df) and vegetation types. They include cloud forest (Henri Pittier), as well as highly disturbed habitats such as a coffee plantation (La Mucuy) and a small patch of *Passiflora* on the road margin in agricultural land (Las Playitas). In one case (Paseo los Pinos near the city of Mérida), *J. radians* im-

matures were found on their host in a vacant lot within a residential area.

The species seems to occur throughout the year; our collecting dates include the months of May, June, July, September, October, and December of 1992, as well as February and March of 1993.

**Foodplant.** We collected *Josia radians* on four *Passiflora* species. It was most frequently found on *P. capsularis* L. (subgenus *Plectostemma*), a widespread species that occurs from Guatemala south to central Brazil and Paraguay up to 1900 m, and throughout the Greater Antilles. At Las Playitas (Fig. 39), the highest elevation so far known for *J. radians* (2250 m), larvae were collected on *Passiflora manicata* Jussieu (subgenus *Granadillastrum*). This plant is known from western Venezuela east to Colombia and south to northern Peru between 1500 and 2500 m elevation. The third *Passiflora* used by *J. radians* is *P. cuneata* (subgenus *Plectostemma*), one of the hosts for *Josia gopala* (see below). Eggs of *J. radians* also were found on *P. rubra* L. (subgenus *Plectostemma*). *Passiflora rubra* is widespread, occurring throughout the West Indies, from Venezuela and Colombia south to Bolivia, and in eastern Brazil. *Passiflora rubra* and *P. capsularis* are close relatives and difficult to distinguish (Killip 1938, Holm-Nielsen 1988, Vanderplank 1991). Our identifications were confirmed by comparison of flowers and fruits.

**Egg.** Diameter = 0.91–0.98 mm ( $n = 12$ ). Eggs are laid singly. Duration: 7 to 8 days. Development time from egg to adult = 40–45 days.

**First Instar.** Head entirely black, except clypeus white. First instars of *J. radians* differ from the other species we studied in the following: antennal segments 1 and 2 short (Fig. 48); thoracic legs with tarsal setae elongate, apex of TS3 emarginate (Fig. 49); thorax with a red dorsal patch on T2 (Fig. 56); segments A1, A3 and A8 ringed with reddish, segments A5 and A10 with a red dorsal patch, A7 with a red lateral patch below spiracle (Fig. 56). Body length = 5.73–6.01 mm ( $n = 3$ ); head width = 0.54–0.57 mm ( $n = 6$ ).

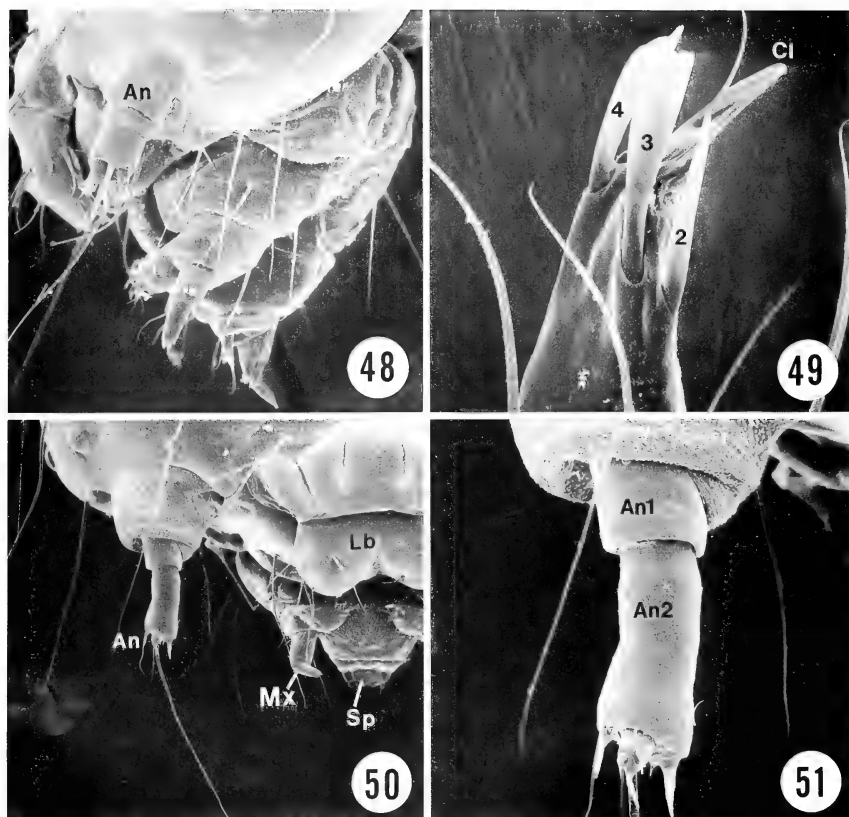
**Second and Third Instars.** Similar in color and setal pattern to final instar. Head widths: 2nd = 0.90–0.91 mm ( $n = 6$ ); 3rd = 1.40–1.44 mm ( $n = 6$ ).

**Final (Fourth) Instar.** Head shiny black with white front, wide white regions extending along ecdysial lines down to antenna, and a pair of lateral white stripes, each from vertex to stemmata, widening below (Fig. 54); antenna with segment 2 approximately twice the length of segment 1 (Fig. 51). Prothoracic shield with anterolateral angles produced, an unpigmented medial seam (Fig. 55); ground color of thorax and abdomen reddish maroon, with a complex white and yellow pattern overlying it (Fig. 16); lateral and dorsal light-colored areas reticulate (Figs. 52, 53); venter entirely white; dorsal red portions more heavily pigmented in an alternating pattern on segments T2, A1, A3 and A5; segment A9 conspicuous, entirely white above (Figs. 16, 53). Tarsal setae (Fig. 57) similar to *Thirmida discinota*. Pattern of primary setae on thorax and abdomen (Figs. 52, 53) similar to *J. aurifusa* and *J. turgida*; lateral plate of A10 proleg base with approximately 9 setae. Body length = 28–30 mm; head width = 2.13–2.22 mm ( $n = 5$ ).

**Pupa.** Cremaster (Figs. 58–60) conical, with a row of longitudinal striae circling base and two more distal concentric rings of reticulate striae; eight stout, hook-shaped setae. The pupal stage lasted 14 days.

**Adult.** FW length = 16.0–19.0 mm. Head orange-yellow with vertex, antenna and scales behind eye black; pectinations of male antenna moderately long; labial palpus

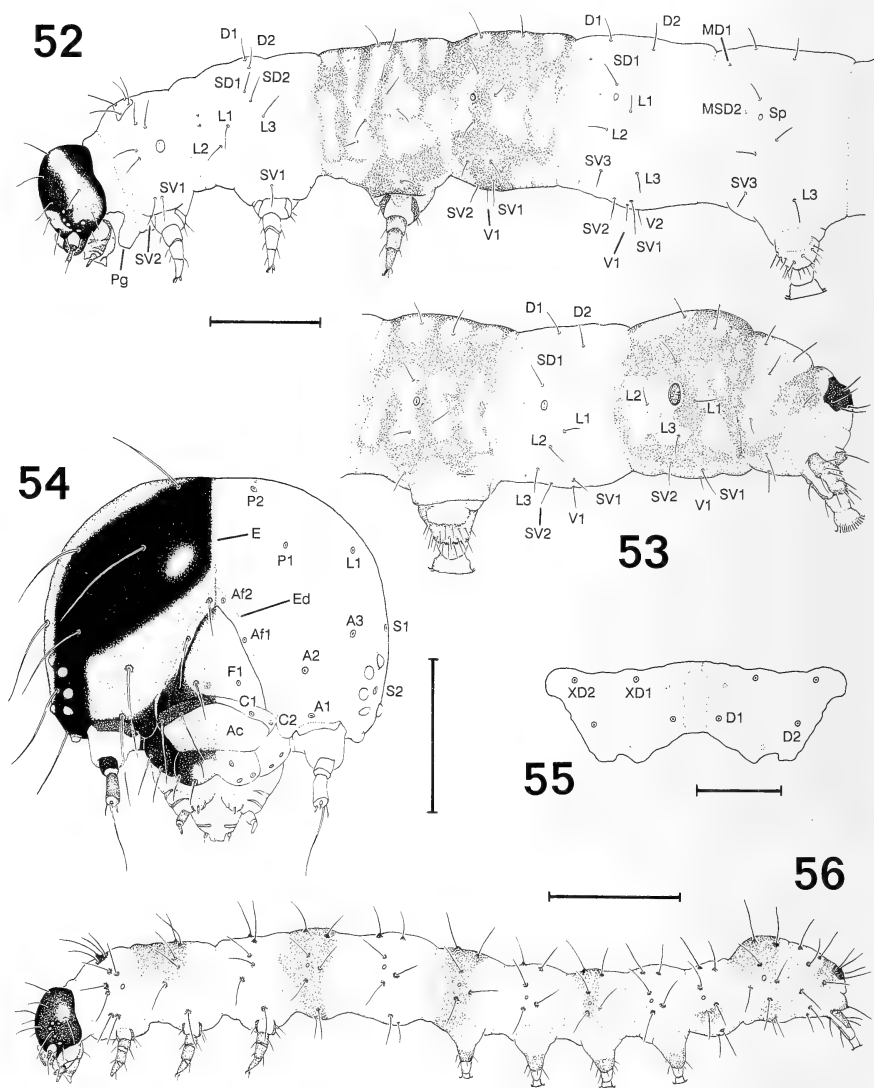




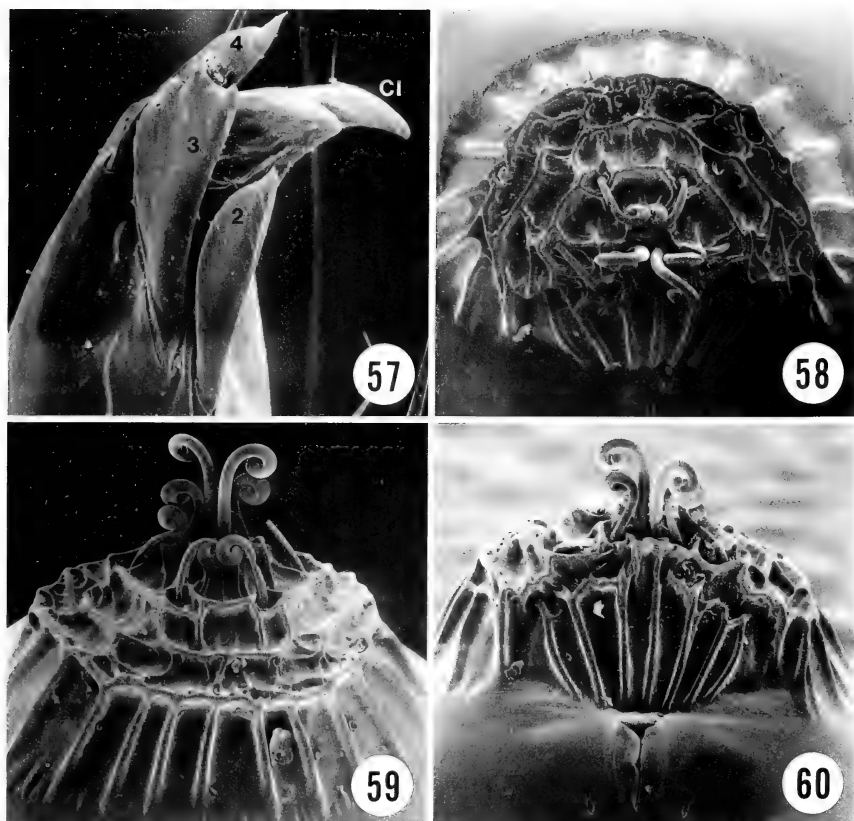
FIGS. 48-51. Scanning electron micrographs of *Josia radians* larvae. **48**, Ventral portion of first instar head, lateral view ( $\times 254$ ); **49**, Tarsus of right metathoracic leg of first instar, mesal view, showing tarsal setae ( $\times 800$ ); **50**, Ventral portion of fourth instar head, frontal view of right side ( $\times 68$ ); **51**, Right antenna of fourth instar, frontal view ( $\times 200$ ). [An = antenna; Cl = tarsal claw; Lb = labrum; Mx = maxillary palpus; Sp = spinneret; 2, 3, 4 = tarsal setae 2, 3, and 4.]

porrect, exceeding front; palpus relatively wide, segment 1 yellow, segment 2 black with yellow scales on venter, segment 3 black. Dorsum of thorax black with orange-yellow stripe on each side running from patagium to abdomen; tegula black in lateral half, yellow along mesal half, with fringe of long yellow scales distally; lateral portions of thorax mostly black, orange-yellow below wing bases; legs black, buff scales on dorsal surfaces; anterior surfaces of forecoxa light buff. FW and HW (Figs. 28, 29) black with thin, longitudinal orange-yellow stripe from base to within 1 mm of outer margin, stripe slightly wider in female; FW and HW costa orange-yellow from base to approximately two thirds out; HW anal margin orange-yellow; longitudinal stripe of FW wider and more diffuse below. Abdomen black with orange-yellow lateral stripe on each side, stripe becoming gray at caudal margin of A8; venter of abdomen whitish buff.

**Discussion.** The moths we reared match the male holotype of *Josia radians* Warren (BMNH) in wing pattern and genitalic morphology.



FIGS. 52-56. Larval stages of *Josia radians*. **52**, Head, thorax, and segments A1-A3 of fourth instar, lateral view; **53**, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); **54**, Head of fourth instar, frontal view (scale line = 1 mm); **55**, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm); **56**, First instar, lateral view (scale line = 1 mm). [A = anterior seta; Af = adfrontal seta; C = clypeal seta; E = epicranial suture; Ed = ecdysial line; F = frontal seta; MD = dorsal proprioceptor seta; P = posteriodorsal seta; Pg = prothoracic gland; S = stemmatal seta; Sp = spiracle; XD = XD seta; for other symbols see "Methods."]



FIGS. 57–60. Scanning electron micrographs of immature stages of *Josia radians*. 57, Tarsus of right T3 leg of fourth instar larva, mesal view, showing tarsal setae 2, 3, and 4 ( $\times 358$ ); 58, Cremaster, posterior view ( $\times 69$ ); 59, Cremaster, dorsal view ( $\times 73$ ); 60, Cremaster, ventral view ( $\times 71$ ). [Cl = tarsal claw.]

However, *J. radians* belongs to a group of closely related species that includes *J. ligata* Walker, *J. frigida* Druce, and *J. fustula* Warren. Identifications in this complex are extremely difficult (Forbes 1931).

#### *Josia gopala* Dognin, 1891

**Distribution.** *Josia gopala* is known only from the State of Mérida, Venezuela (AMNH, BMNH, MIZA, NMNH, ZMH). The locality label on the female holotype (NMNH) reads “Mérida, Venezuela; Terre Temperee,” the latter (in French) probably referring to a temperate habitat. Based on museum label data and on data we have accumulated, *Josia gopala* occurs within a fairly restricted altitudinal range, between 2000 and 3000 meters. Although *J. gopala* is rare in museum collections,

previously known from less than 20 specimens, the moth can be quite common in Mérida.

**Collecting Localities.** Eggs and larvae were collected at four cloud forest localities. Two sites, close together in Asentamiento Monterrey, El Valle (LM-mf) at 2300 and 2350 m elevation, were visited on 14 and 23 June 1992, 16 August 1992, and 7 March 1993. One of these is along a cloud forest margin bounded by agricultural land and dispersed human habitations (Fig. 40), while the other is in a pine plantation in what was formerly cloud forest. Our other two sites were along the road to El Morro (2150 m), visited on 6 September 1992 (LM-mf), and in Parque Nacional Sierra Nevada, La Mucuy (2300 m), visited on 12 October 1992 (LM-wf). The species seems to be restricted to the borders of forested habitats.

**Foodplant.** *Josia gopala* was discovered feeding on two *Passiflora* species. Eggs were collected on *Passiflora cuneata* Willdenow (subgenus *Plectostemma*) growing in the shaded forest margins. This *Passiflora* is known from the mountains of central Venezuela east to the Cordillera Santa Marta and eastern Cordillera of Colombia at elevations between 700 and 3800 m. Caterpillars also were found on *Passiflora gritensis* Karsten (subgenus *Granadilla*). In one case, the *P. gritensis* plants were growing in a pine plantation. *Passiflora gritensis* is known only from western Venezuela at altitudes near 2500 m. These two *Passiflora* species occur together at the Monterrey sites. Females of *J. gopala* tend to oviposit on tender, lower leaves of the host near the ground, especially on the leaves of seedlings or new shoots.

**Egg.** Diameter = 0.86–1.01 mm ( $n = 18$ ). Duration: 7 to 8 days. Eggs are laid individually, not in clusters. Development time from egg to adult = 52–56 days.

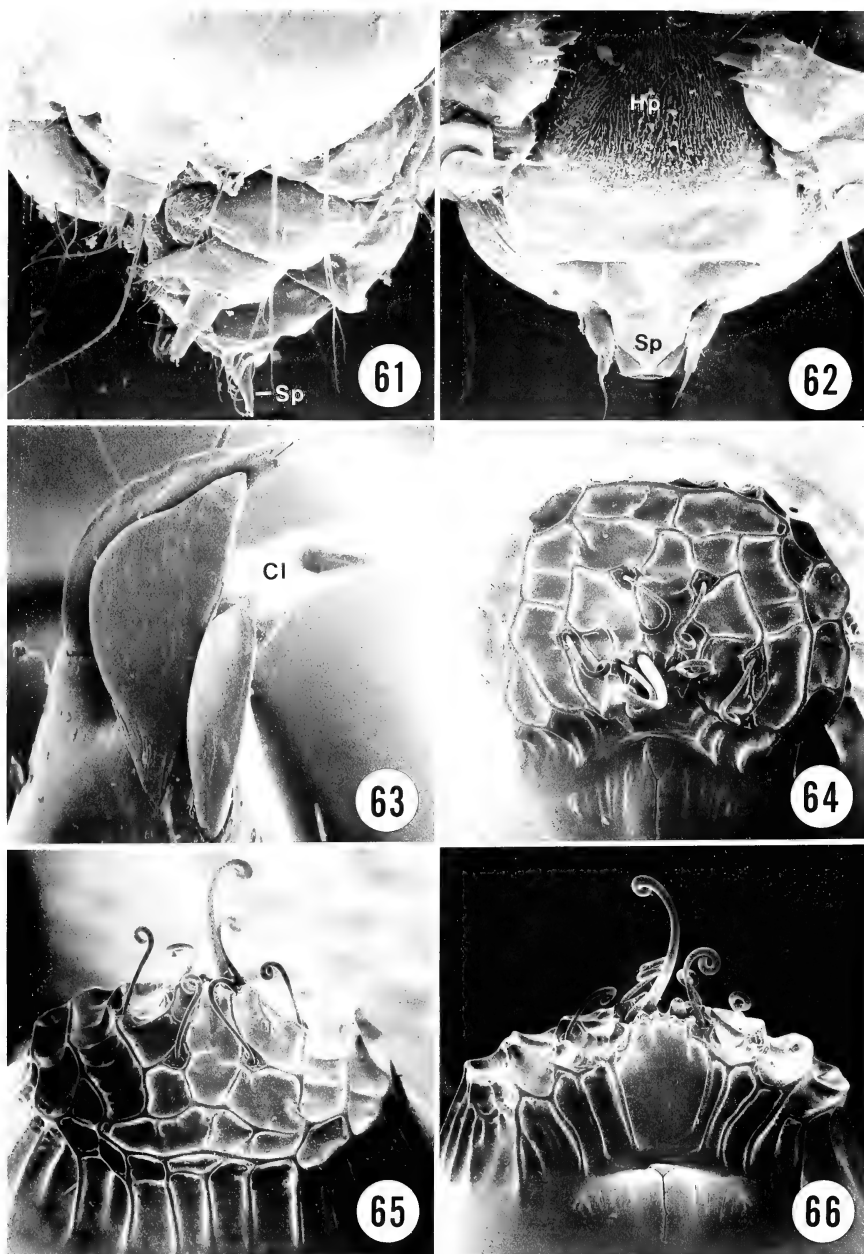
**First Instar.** Head dark brown except for white clypeus, and small light brown patches at ventral angles of front beyond ecdysial lines. General morphology and primary setae (Figs. 61, 71) similar to other Josiini. Body length = 4.38–5.19 mm; head width = 0.57–0.62 mm.

**Second and Third Instars.** Similar in pigmentation and setal pattern to final instar. Head widths: 2nd = 0.89–0.95 mm; 3rd = 1.39–1.50 mm ( $n = 4$ ).

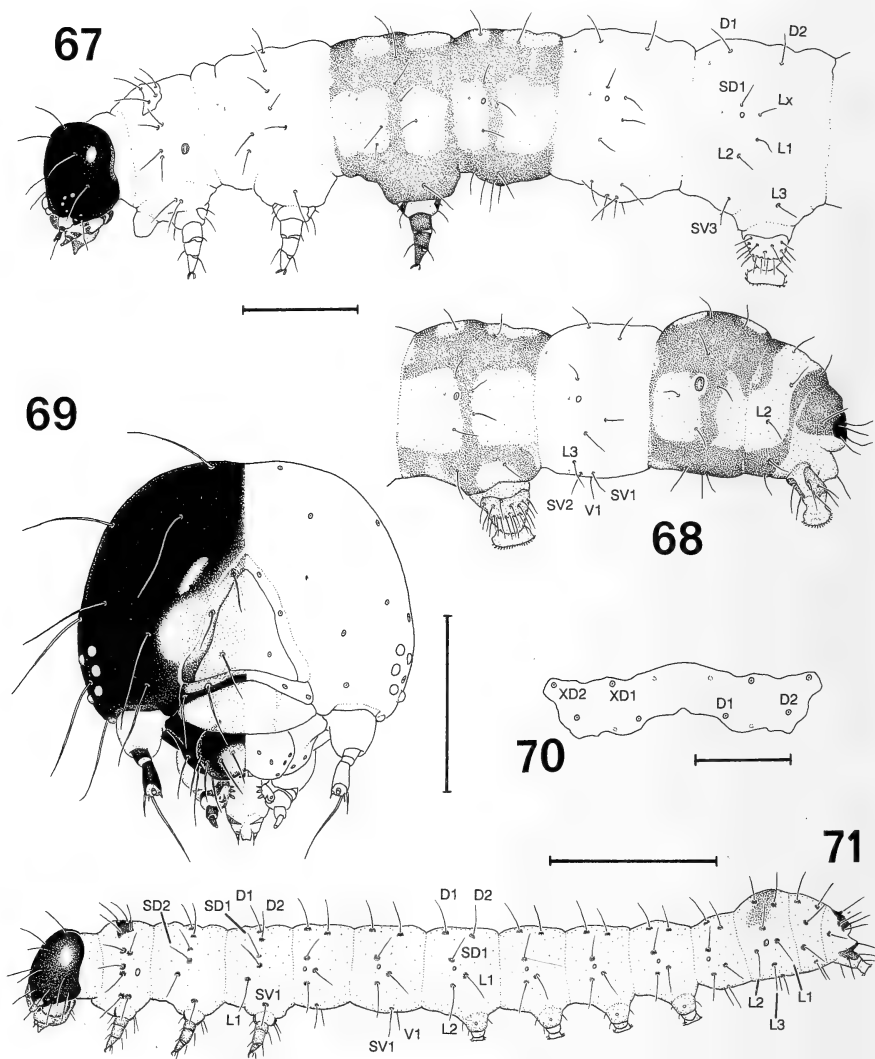
**Final (Fourth) Instar.** Head shiny black except for white frons and clypeus, and two ovoid white patches on either side of ecdysial lines (Fig. 69); antenna with segment 2 approximately twice the length of segment 1. Prothoracic shield narrow, no medial seam (Fig. 70); ground color of thorax and abdomen reddish maroon, overlying pattern simple, white and yellow (Fig. 17); light-colored lateral and dorsal areas roughly rectangular in shape (Figs. 67, 68); venter entirely white; segment A9 conspicuous, entirely white above. Tarsal setae (Fig. 63) with TS2 lanceolate, TS3 broad and leaf-shaped, TS4 sword-shaped with apex acute. Setal pattern on T1–A10 (Figs. 67, 68) similar to last instars of other *Josia* species except: a novel L seta (seta "Lx" in Fig. 67) present on segments A2–A6, located between SD1 and L1; lateral plate of A10 proleg base with only 4 setae ( $n = 9$  in other *Josia* species). Body length = 25–26 mm; head width 1.9–2.13 mm ( $n = 5$ ).

**Pupa.** Cremaster (Figs. 64–66) short, somewhat flattened distally, fluting irregular; eight delicate, widely spaced, hook-shaped setae. Duration: approximately 19 days. The pre-pupal larvae weave a shelter of leaves and crawl into it to pupate (2 observations).

**Adult.** FW length = 16.5–17.5 mm. Head, thorax, and abdomen dark charcoal blue-



FIGS. 61-66. Scanning electron micrographs of immature stages of *Josia gopala*. **61**, Ventral portion of first instar head, lateral view ( $\times 294$ ); **62**, Maxillary and hypopharyngeal complexes of fourth instar larva, frontal view ( $\times 215$ ); **63**, Tarsus of right prothoracic leg of fourth instar larva, mesal view ( $\times 468$ ); **64**, Cremaster, posterior view ( $\times 81$ ); **65**, Cremaster, dorso-posterior view ( $\times 76$ ); **66**, Cremaster, ventral view ( $\times 81$ ). [Cl = tarsal claw; Hp = hypopharynx; Sp = spinneret.]



FIGS. 67-71. Larval stages of *Josia gopala*. **67**, Head, thorax, and segments A1-A3 of fourth instar, lateral view; **68**, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); **69**, Head of fourth instar, frontal view (scale line = 1 mm); **70**, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm); **71**, First instar, lateral view (scale line = 1 mm). [Lx = novel L seta; see text.]

gray, a lighter lateral stripe on each side of abdomen; pectinations of male antenna short; labial palpus narrow and porrect, slightly exceeding front. Wings (Figs. 30, 31) with outer margins dark bluish black. FW with a wide, yellow longitudinal stripe extending from base to fork of  $M_3$  and  $CuA_1$ , just beyond DC; posterior margin light gray below; costa black; HW with large yellow central area; anterior margin light gray above; dorsal and ventral wing surfaces with essentially the same pattern.

**Discussion.** The species *gopala* was described by Dognin (1891) in *Flavinia*, a genus in the Geometridae (Watson et al. 1980), but was moved by Prout (1918) to *Josia*. The moth can be separated from most other *Josia* by the wide, truncate, longitudinal FW stripe which extends for only two thirds the wing length (Figs. 30, 31; Hering 1925). The larva exhibits a relatively simple pattern, with roughly rectangular, yellow and white patches on each segment laterally and dorsally (Fig. 17). The last instar is unique among the known species of Josiini in its possession of an extra L seta on segments A2–A6 (Figs. 67, 68).

Based on similarities of wing pattern (Forbes 1931) and genitalia (JSM, unpubl.), the closest relatives of *Josia gopala* are *J. patula* Walker and *J. gephyra* Hering. These two are slightly larger species (FW length = 18.5–21.0 mm) with the yellow forewing stripe narrower and extending further out (Hering 1925). *Josia patula* is fairly well represented in museum collections, being known from Choachi, Villavicencio, and Bogotá, Colombia (BMNH, CMNH, CUC, NMNH, ZMH). *Josia gephyra* is rare; we have seen only four specimens (NMNH, BMNH), all collected at the type locality, Cañon del Monte Tolima, Colombia. This is a high altitude site; one of these specimens was caught at 4700 m (BMNH). Assuming the label is correct, this is the highest altitude recorded for any species of Dioptriinae.

### *Josia aurifusa* Walker, 1854

**Distribution.** *Josia aurifusa* appears to be endemic to Venezuela, occurring from the state of Aragua west to Tachira (AMNH, CMNH, MIZA, MNHN). The label on the male holotype (BMNH) gives the locality simply as "Venezuela."

**Collecting Localities.** We collected eggs, larvae, and adults of *Josia aurifusa* at two localities in the Parque Nacional Henri Pittier (PM-wf) in the State of Aragua. On 22 March 1992, we collected six eggs on *Passiflora* leaves at Rancho Grande Field Station (1100 m). We also collected 16 eggs and one final instar larva on 2 April 1992, near a stream crossing the road from Maracay to Choroni (860 m) on the northern slope of the mountains (Fig. 73). An adult female, collected at the second locality, produced eight eggs from which reared material was obtained. Eggs of the species also were collected at a third locality on the road from Barinas to Santo Domingo at Quebrada El Alambique (1250 m; also PM-wf) in the State of Barinas. All three are cloud forest sites. Eggs and larvae of what turned out to be an extremely dark form of *Josia aurifusa* (Fig. 34) were found in the state of Mérida at Puente Victoria (540 m, T-mf) on the road from Mérida to El Vigía (Fig. 41).

**Foodplant.** *Josia aurifusa* was found on two *Passiflora* species. At the Aragua localities it fed on *P. rubra*, while at Puente Victoria it was on *P. capsularis*. Both plant species are discussed under *J. radians* (above).

**Egg.** Diameter = approximately 0.7–0.8 mm; laid either singly or in small clusters of up to nine eggs. Duration: 4–5 days. Development time from egg to adult = 59 days.

**First Instar.** Head dark brown, slightly lighter on front, antenna short (Fig. 79); body lacking pigment (Fig. 78). Body length = 4.11 mm ( $n = 1$ ); head width = 0.49–0.51 mm ( $n = 5$ ).

**Second and Third Instars.** Similar in markings and setal pattern to final instar. Head widths: 2nd instar = 0.82–0.83 mm; 3rd instar = 1.25–1.30 mm ( $n = 5$ ).

**Final (Fourth) Instar.** Head white, with wide, brownish black frontolateral stripes extending from stemmata up to epicranial suture, stripes widening near suture (Fig. 76); labrum black with a white central region; antenna (Figs. 80, 81) with segment 2 relatively short, less than twice the length of segment 1. Prothoracic shield (Fig. 77) with an unpigmented medial seam, anterolateral angles produced, curled inward; ground color of thorax and abdomen reddish maroon (Fig. 18), red colored regions lightly spotted with white; yellow-white dorsal and lateral patches irregularly shaped (Figs. 74, 75), roughly rectangular, relatively small (compared to *J. turgida*, below); seta L3 on A3–A6 surrounded by a smallish white spot (Fig. 75); venter white with red, transverse connecting lines on A1 and A2; segment A9 conspicuous, entirely white above (Fig. 18). Tarsal setae as in *Josia gopala*. Primary setae (Figs. 74–76) as in *Josia radians*; lateral plate of A10 proleg base with approximately 9 setae. Body length = 24.5–26.0 mm; head width = 1.86–1.98 mm ( $n = 6$ ).

**Pupa.** Cremaster blunt, with uneven longitudinal flutes at base and irregular striae on distal flattened portion; strongly concave ventrally; eight hook-shaped setae present. Duration: 10 days.

**Adult.** FW length = 13.5–17.0 mm. Antenna black; head mostly black, face white with front blackish gray; scales at antennal base white; pectinations of male antenna moderately long; labial palpus porrect, relatively long and thin, extending well beyond front; basal three fourths of palpus segment 1 white, rest of palpus black. Dorsum of thorax black, an orange stripe on each side running from patagium to base of abdomen; tegula orange, black at base; lateral portions of thorax orange; coxa black laterally, white on anterior surfaces; legs dark gray, tibiae whitish-buff below. FW black with a wide, orange longitudinal stripe from base to within 2 mm of outer margin (Figs. 35, 36), stripe tapering gradually toward apex; Rs entirely black through orange stripe; HW (Figs. 35, 36) black with caudal two thirds orange; orange region with a diffuse, black, wedge-shaped streak along vein 2A from near base, widening toward outer margin; costa of HW light orange in basal two thirds. Abdomen black with wide, orange lateral stripes, stripes becoming buff at caudal margin of A8; venter white. HW almost entirely black in some specimens (Fig. 34), with a diffuse orange streak along CuA2, and anal margin a combination of orange and black scales.

**Discussion.** Walker's description of *aurifusa* (1854: 293) and the holotype (BMNH) match our material from Choroní. However, *Josia aurifusa* is a variable species (Hering 1925); our specimens from Puente Victoria are extremely dark (Fig. 34). Four names have been synonymized with *aurifusa*, all of which currently stand as either forms or aberrations (Bryk 1930). The phenotypes associated with these names vary in the shape of the longitudinal forewing stripe and in the amount of black in the hind wing. We recognize one of those, "form" *turgida* Warren, as a distinct species (see below).





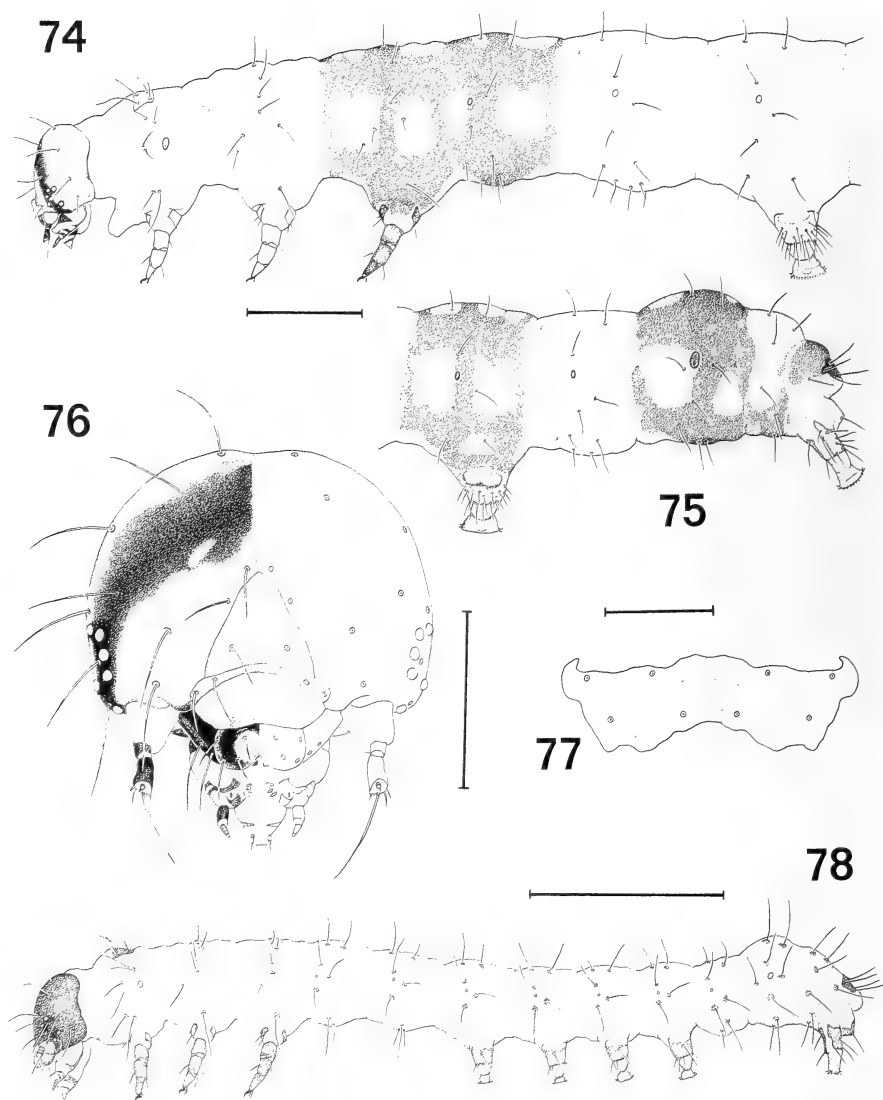
FIGS. 72, 73. Collecting sites for *Josia* species. 72, Beside the road to La Mesa de Ejido, State of Mérida, 1.8 km from the turnoff in the Panamerican Highway on the way to Jaji (1560 m), a locality for *Josia radians*; 73, Along the road from Maracay to Choroni (860 m), State of Aragua, a locality for *Josia aurifusa*. Photographs by L. Daniel Otero.

*Josia turgida* Warren, 1905b, revised status

**Distribution.** Like *Josia aurifusa*, *J. turgida* appears to be endemic to Venezuela. The species is sympatric with *J. aurifusa*, but it has been recorded from further east (Puerto la Cruz, Anzoátequi; CMNH), and does not seem to extend as far west; our western-most record is Altamira in the state of Barinas (LDO, collector). The type locality is Valencia, Venezuela (State of Carabobo).

**Collecting Localities.** Eggs and first instar larvae of *Josia turgida* were found along the road to Altamira in the State of Barinas, approximately 2.6 km from the turnoff on the Barinas to Santo Domingo road (645 m; T-mf). Eleven eggs were collected on 28 June 1992, and 14 eggs and five first instar larvae on 13 September 1992. Eggs of the species also were collected on the road from Barinas to Santo Domingo at Quebrada El Alambique (1250 m) in the State of Barinas.

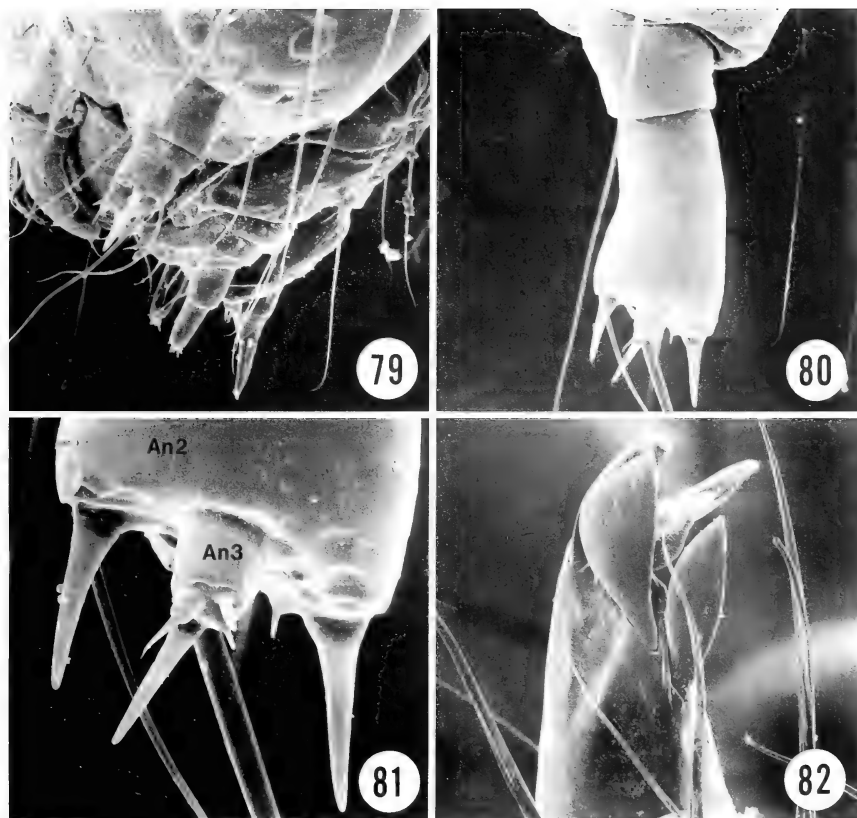
**Foodplant.** The known hostplants are *Passiflora capsularis* and *P. rubra*. These *Passiflora* species also are used by *J. aurifusa* and *J. radians*. Larvae were collected from plants growing in secondary vegetation along road margins.



FIGS. 74-78. Larval stages of *Josia aurifusa*. 74, Head, thorax, and segments A1-A3 of fourth instar, lateral view; 75, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); 76, Head of fourth instar, frontal view (scale line = 1 mm); 77, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm); 78, First instar, lateral view (scale line = 1 mm).

**Egg.** Diameter = 0.7 to 0.8 mm; found in small clusters of two to nine eggs. Duration: 4 days. Development time from egg to adult = 42 days.

**First Instar.** Similar to other Josiini; head dark brown, slightly lighter on front. Body length = 4.05 mm; head width = 0.48 mm (n = 1).

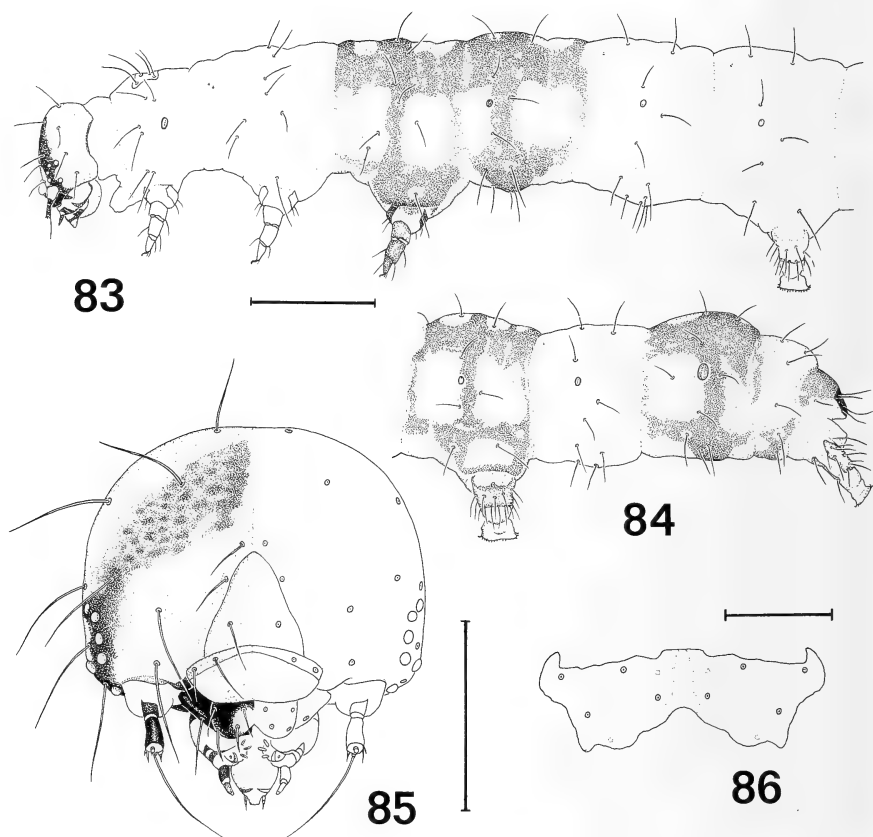


FIGS. 79–81. Scanning electron micrographs of *Josia aurifusa* larvae. **79**, Ventral portion of first instar head, lateral view ( $\times 350$ ); **80**, Right antenna of fourth instar, frontal view ( $\times 266$ ); **81**, Distal portion of fourth instar antenna showing segments 2 and 3 ( $\times 734$ ). [An = antennal segment.]

FIG. 82. Right tarsus on T2 of fourth instar *Josia turgida* larva, mesal view ( $\times 292$ ).

**Second and Third Instars.** Similar in coloring and setal pattern to final instar. Head widths: 2nd instar = 0.81–0.83 mm; 3rd instar = 1.22–1.26 mm ( $n = 5$ ).

**Final (Fourth) Instar.** Head (Fig. 85) white with wide, brown, irregularly patterned frontolateral stripes extending from stemmata up to epicranial suture, stripes widening near suture; labrum black with a white central region; antenna with segment 2 relatively short, less than twice the length of segment 1. Prothoracic shield with an unpigmented medial seam, anterolateral angles produced, curled inward (Fig. 86). Ground color of thorax and abdomen reddish maroon (Fig. 19); red colored regions lightly spotted with white (Figs. 83, 84); white spots present at bases of primary setae; yellow-white dorsal and lateral patches larger than in *J. aurifusa*, margins smoother; venter white, with red transverse connecting lines on A1 and A2; L3 on A3–A6 surrounded by a large white patch; segment A9 conspicuous, entirely white above (Fig. 19). Tarsal setae (Fig. 82) similar to *Josia gopala*. Primary setae (Figs. 83–85) as in *J. radians* and *J. aurifusa*; lateral plate of A10 proleg base with approximately 9 setae. Body length = 24.0–25.0 mm; head width = 1.88–1.94 mm ( $n = 3$ ).



FIGS. 83-86. Larval stages of *Josia turgida*. **83**, Head, thorax, and segments A1-A3 of fourth instar, lateral view; **84**, Segments A6-A10 of fourth instar, lateral view (scale line = 2 mm); **85**, Head of fourth instar, frontal view (scale line = 1 mm); **86**, Prothoracic shield of fourth instar, dorsal view (scale line = 0.5 mm).

**Pupa.** Cremaster similar to *J. aurifusa*, slightly less concave ventrally; eight hook-shaped setae present. Duration: approximately 17 days.

**Adult.** FW length = 14.0-17.0 mm. Head and antenna black; face white with front blackish gray; scales at antennal base white; pectinations of male antenna moderately long; labial palpus porrect, relatively long and thin, extending well beyond front; basal three fourths of segment 1 white, rest of palpus black. Dorsum of thorax black, an orange stripe on each side running from patagium to base of abdomen; tegula mostly orange, black at base; lateral portion of thorax orange; coxa black on lateral surface, white on anterior surface; legs dark gray, tibiae whitish-buff below. FW black with a wide, orange longitudinal stripe from base to within 2 mm of outer margin (Figs. 32, 33); stripe tapered, slightly irregular along anterior margin near apex; Rs black at base, orange beyond; HW (Figs. 32, 33) orange with upper angle black from a point near upper corner of DC to outer margin; a diffuse black patch along 2A near outer margin. Abdomen black with wide, orange lateral stripes, stripes becoming buff at caudal margin of A8; venter white.

**Discussion.** *Josia turgida*, described by Warren (1905b:314) in the subfamily Cylopodinae (Geometridae), was considered a form of *J. aurifusa* by Hering (1925) and subsequent authors, but we here elevate it to species status.

Although *J. turgida* and *J. aurifusa* are extremely close, we found what seem to be reliable differences between these two sympatric species. Adults of *J. turgida* generally are more orange than those of *J. aurifusa* (compare Figs. 32–36). The FW stripes are wider and the black portion of the HW does not reach the wing base. In *J. turgida* there is usually a prominent orange macula on the dorsum of the mesothorax, while in *J. aurifusa* this area is either entirely black, or has a very small, faint orange spot. There are also subtle differences between the larvae. The yellow-white lateral patches on the thorax and abdomen are larger in *J. turgida* than in *J. aurifusa* (compare Figs. 74, 75 with 83, 84), especially those surrounding seta L3 on the proleg-bearing segments. The head stripes of *J. turgida* are lighter in color, and the pigmentation is more irregular (Fig. 85). The larvae of *J. turgida* are thus generally lighter in color than those of *J. aurifusa*.

*Josia aurifusa* and *J. turgida*, together with their various color forms, belong in a species complex with *Josia auriflua* Walker, known from the western Andes of Colombia south to Bolivia. To further complicate matters, three Dognin names—*inaequiflexa*, *scalata*, and *flavipars*—are listed as subspecies of *J. auriflua* in Bryk (1930). The entire *aurifusa* complex poses a serious taxonomic challenge; wing pattern variation seems to merge, and genitalic differences are not always clear-cut (JSM, unpubl.).

## CONCLUSIONS

Based on our findings for these five Venezuelan Josiini and on published reports for other taxa, we now can offer a general summary of biological characteristics for the tribe.

The species occur over a wide range of elevations, from lowland jungle to shrubby, high altitude sites in the Andes of South America and the Central Cordillera of Central America. *Cyanotricha bellona* has been recorded at 4000 m in Peru (BMNH), and *Josia gephyra* was collected in Colombia at 4700 m (see discussion of *J. gopala* above). Josiini are most common in secondary forests and disturbed habitats, but they also occur in pristine environments. Even in primary forests, however, they seem to favor light gaps, forest edges, and stream margins, perhaps due to the higher frequency of their passifloraceous hosts in such habitats. In this study, immatures of *Josia radians* were found on *Passiflora* growing in a coffee plantation, and at another site close to the city of Mérida within the confines of a housing development.

At least one species is of economic importance. *Cyanotricha necyria* is an occasional pest in commercial fields of *Passiflora mollissima* in the Andes of Colombia, Ecuador, and Peru (Castaneda 1956, Martin & Nakasone 1970). Markin et al. (1989) have studied *C. necyria* and other Josiini as potential biological control agents of *P. mollissima*, a damaging weed in Volcano National Park, Hawaii.

Members of the Josiini share many life history features, some of which apparently are unique to the tribe. For example, unlike most Lepidoptera, which have either five or six larval instars, all Josiini so far studied have only four (Spitz 1931, d'Almeida 1932, Markin et al. 1989). The number of larval instars in other subfamilies of the Notodontidae is five (Packard 1895), and published reports for Dioprinae outside the Josiini indicate that five is typical there as well (Herbert 1920, Wolda & Foster 1978).

In the species we observed, and in *Cyanotricha necyria* (Markin et al. 1989), first instars often feed together on the same leaf, while subsequent instars feed individually. These observations agree with previous work showing this to be a general trend for the Notodontidae (Godfrey et al. 1989). Associated with this trend is a developmental change whereby the first instar mandibular margin is serrate, while that of later instars is smooth (Godfrey et al. 1989, Dockter 1993).

Josiini exhibit a characteristic pupation behavior. The pre-pupal caterpillar makes a shelter, using strong silk threads to weave pieces of leaves or debris together. The larva then pupates in this enclosure, normally within a few days after its construction. In the absence of such materials, the larva builds a flimsy silk net. Pupation usually takes place off the hostplant, but in one instance we found a pupa on its *Passiflora* host.

Several characteristics distinguish the immatures of Josiini from those of heliconiines, the only other Lepidoptera common on *Passiflora*. *Heliconius* eggs, deposited singly or occasionally in large clusters, are somewhat cylindrical with prominent surface sculpturing, and are usually yellow, orange, or red (Beebe et al. 1960, Benson et al. 1976, DeVries 1987). They are generally larger than the eggs of Josiini. Female Heliconiinae frequently oviposit on new leaves or on shoots near the meristem, whereas josiines tend to lay on older leaves closer to the ground, always on the leaf undersurface. The eggs of *Eueides* (Heliconiinae) are similar to those of Josiini in that they are frequently laid on the undersurface of mature leaves, and they are small and green. However, *Eueides* eggs differ in having prominent surface sculpturing (JSM pers. obs.).

Josiine larvae lack projections on the body. They exhibit the shagreened cuticle characteristic of other Dioprinae (Fracker 1915, Forbes

1939, Miller 1991), a trait that can be seen with the aid of a hand-lens. The caterpillars thus are impossible to confuse with heliconiine larvae, which are usually greenish white overlaid with various dark patterns, and which have long, spiny projections on the head, thorax, and abdomen (Beebe et al. 1960, Brown 1981, DeVries 1987).

Adult josiines can be recognized in the field by their erratic, fluttering flight and bright coloration. After landing first on the upper surface of a leaf, they often move quickly out of sight to the underside. Upon close examination, the unusual metathoracic tympanum and wing venation can be used as diagnostic features to distinguish them from all other Lepidoptera.

Having here described the immature stages of four *Josia* species and *Thirmida discinota*, we hope to discover life histories for still other taxa. We urge field workers collecting on or around *Passiflora* to learn to recognize and collect Josiini. A long-term goal is to accumulate enough hostplant data to compare patterns in the Josiini with those that have been described in the literature for the Heliconiinae (Benson et al. 1976). Because the immature stages appear to be a rich source of characters, their discovery also will benefit greatly systematic studies on the Dioptriinae.

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## A SIMPLE PORTABLE TRAP FOR MIGRATING BUTTERFLIES

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**ABSTRACT.** An economical, easily built, 4-m wide trap for migrating butterflies was developed and tested. Made of thin-walled electrical conduit, nylon rope, and polypropylene netting, a "simplex" trap can be erected or taken down quickly, rolled into a compact bundle, and carried by one person.

**Additional key words:** migration, *Phoebis sennae*, *Agraulis vanillae*, Florida.

Migrating butterflies are peculiarly subject to trapping because they generally fly in a straight line near the ground, and upon encountering an obstacle, they attempt to fly over it rather than change directions. Starting in 1975, a series of traps was developed that took advantage of this behavior (Walker 1978, 1985b, Walker & Lenczewski 1989). These were used to monitor butterfly migrations in the southeastern United States (Walker 1985a, 1991, Walker & Riordan 1981, Lenczewski 1992).

Since 1986, one of us (JJW) has headed a project to promote the study of butterfly migration by high school science students throughout Georgia. A major goal of these studies has been to mark and release migrating *Phoebis sennae* (L.) (Pieridae) and *Agraulis vanillae* (L.) (Nymphalidae) in hopes of documenting their migration routes and distances. As an adjunct to this project, we worked together to develop a trap that was economical, easy-to-build, and effective. We succeeded in satisfying these criteria with a "semi-portable" trap that had a rigid  $3.4 \times 3 \times 1.3$  m frame of lumber and metal tubing (Walker & Whitesell 1993) but soon discovered that such traps, when used on high school grounds, were often vandalized or totally destroyed at night or over weekends. We therefore added the criteria that the traps had to be easily erected, taken down, and moved in and out of school buildings.

### METHODS

An earlier trap was portable (Walker & Lenczewski 1989) but erecting it involved setting and adjusting eight guy ropes and took up to an hour. Furthermore, building it required difficult sewing, sheet metal

work, and cutting and riveting hardware-cloth cages. We conceived, built, and tested a series of much simpler portable traps that shared these features: (1) end supports of just two lengths of thin-walled electrical conduit (EMT), held together by a single eyebolt near the top (permitting the ends to scissor shut when the trap was taken down), (2) the EMT supports of the trap were connected by 4-m lengths of 3.2 mm braided nylon rope, including one 2 m above ground level and two  $\approx 5$  cm apart at the eyebolt, (3) the trap was covered with polypropylene netting glued to the EMT frame and around lengths of rope with silicon caulk, (4) erecting the trap involved opening and positioning the end frames and putting the connecting ropes under tension with a guy attached at each end to the eyebolt (Fig. 1A & B), (5) trapped butterflies were retained in the triangular duct at the top of the trap rather than passing into hardware-cloth holding cages. We called these traps "simplex" traps and built and tested six types.

Five designs of end frames were tested—three sizes of "A-frames" and two sizes of "oblique frames" (Fig. 1C). For convenience, the designs were named by the lengths of the end-frame members expressed to the nearest meter. In pilot tests in fall of 1991, the 3 $\times$ 3 and the 3 $\times$ 5 designs proved inefficient.

The remaining three designs were compared 17 Sep to 21 Oct 1992 with each other and with two permanent traps that had been in service since 1984 (Walker 1985b, 1991). The 5 $\times$ 5 and 4 $\times$ 6 traps were covered with black, nearly invisible, polypropylene netting ( $\approx 8 \times 10$  mm mesh, Tenax Ornex SM®). Two 4 $\times$ 4 traps were tested, one with the black fabric and one with orange, daylight-fluorescent, polypropylene netting ( $\approx 6 \times 6$  mm mesh, Tenax Plurima®). The four traps were set in random order facing NNW in a line beginning at the west end of the permanent traps. The order was rerandomized after each quarter of the migratory season, with the restriction that each trap would occupy each position only once. Traps were serviced every one or two days. Catches by the simplex traps were compared by ANOVA. The permanent traps were excluded from the ANOVA because there was no control for position effects.

## RESULTS

For neither *P. sennae* or *A. vanillae* were the numbers caught in the four simplex traps significantly different ( $P=0.08$  and  $0.85$ ). For both species the greatest total numbers were caught in the 4 $\times$ 4 black trap (80 and 32) and the least in the 5 $\times$ 5 trap (33 and 25). The total catch *per meter* of simplex trap was 14.2 and 7.7 (*P. sennae* and *A. vanillae*) and, of permanent trap, 17.0 and 31.3.

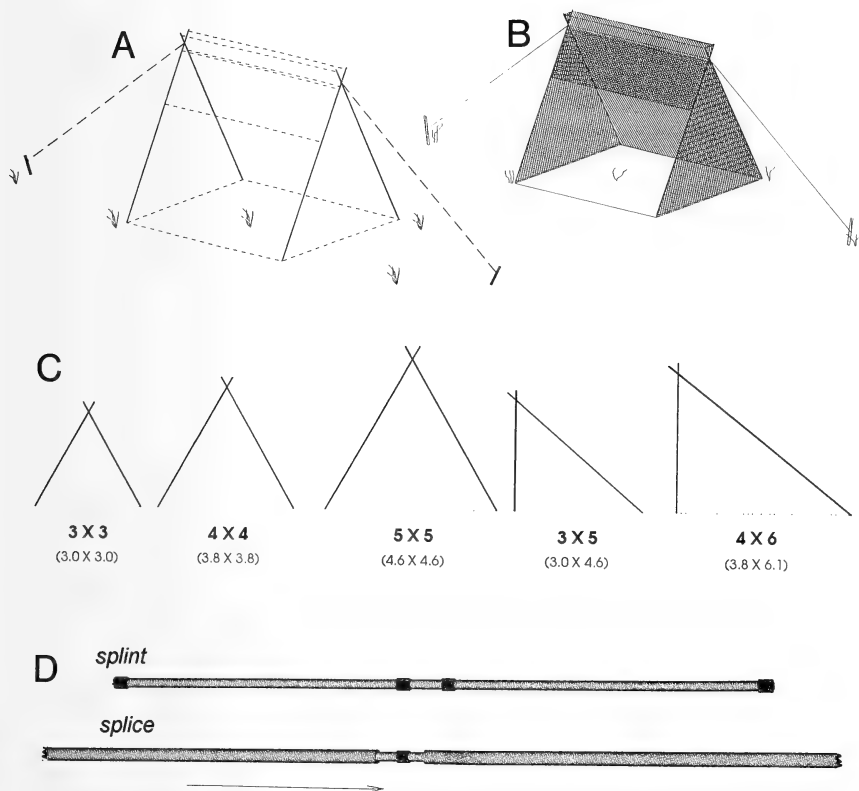


FIG. 1. Portable butterfly trap. A. Frame of simplex trap constructed of EMT (solid lines) and braided nylon rope (dashed lines). B. Same trap covered with polypropylene netting. C. End frame configurations that were tested, with EMT lengths, in m, below. D. Technique for splicing two lengths of EMT. Splint is 40" piece of  $\frac{1}{2}$ " EMT with wrappings of tape in four places. Splice is made by sliding pieces of  $\frac{3}{4}$ " EMT over splint.

## DISCUSSION

Of the simplex designs tested, we recommend the 4x4 traps because they caught as many or more *P. sennae* and *A. vanillae* as larger, harder-to-build-and-service designs. Using the directions included in the appendix of this paper, Georgia high school students and their teachers have built and put in service at least 15 4x4 simplex traps.

The orange polypropylene netting was tested in hopes that it would be a magnet to *P. sennae*, which stops at red flowers (and red taillights in parking lots). It actually caught fewer *P. sennae* and *A. vanillae*, but not significantly fewer. A comparison of the two fabrics on a pair of semi-permanent traps likewise failed to reveal a significant difference

in the catches of *P. sennae*, but the orange caught significantly more *A. vanillae* (Walker, unpublished). A disadvantage of the daylight fluorescent orange fabric is that it makes a trap ultra conspicuous to passersby.

The permanent traps are approximately 60 and 35% efficient at catching migrating *P. sennae* and *A. vanillae* respectively (Walker 1985b). Assuming that their position relative to the permanent traps did not influence the numbers of potential captives or trapping efficiency, the simplex traps caught an estimated 50% of the *P. sennae* they should have intercepted and 9% of the *A. vanillae*. These estimates are likely low because the simplex traps caught significantly fewer migrants when in the two west-most positions than when in the two positions closer to the permanent traps. This may have resulted from trees to the NNW of the west-most positions causing migrants to fly higher as they approached.

Compared to previous traps for migrating butterflies, simplex traps are the least expensive and the easiest to build. They are easy to erect, strike, carry, and store. For the first time, a researcher could, in a single day, set out an extensive line of traps to quantify a migration, and move it to a different transect the next day. Unlike netting used previously, the two types of polypropylene that were tested did not weaken after more than a year in the Florida sun; and because the traps are easy to take down and store, there is no need to leave them outside when not in use. Because the width of the trap is determined by ropes under tension rather than the standard 3m length of EMT crosspieces, simplex traps can take advantage of the full 4 m width of the fabric, increasing the reach of the trap by 33%.

The most serious disadvantage of simplex traps is that they are substantially less efficient in catching *A. vanillae* than the semi-portable traps. Lacking a valved catching cage, simplex traps must be serviced at 1 or 2-day intervals or captured butterflies will escape. Finally, the ease with which they can be taken down means that simplex traps are easily stolen (if left up).

#### ACKNOWLEDGMENTS

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## APPENDIX: BUILDING AND USING A SIMPLEX TRAP

### Materials

- 5 – 10' pcs,  $\frac{3}{4}$ " EMT (electrical conduit)
- 2 – 10' pc,  $\frac{1}{2}$ " EMT [will have 40" pc left over]
- 8 –  $1 \frac{1}{4}$ "  $\times$   $\frac{10}{32}$  machine screws with nuts
- 2 –  $\frac{1}{4}$ " eyebolts 3" long with nuts
- 6 –  $\frac{1}{4}$ " machine washers
- 2 –  $\frac{1}{4}$ "  $\times$   $1 \frac{1}{4}$ " machine bolts with nuts
- 2 tubes transparent silicon caulk
- 42' of 13'-wide,  $\frac{3}{8}$ "-mesh, [filament dia = 0.15 mm], black polypropylene netting. ("Tenax Ornex SM": Geotex Corp., Jessup MD)
- 118½' of  $\frac{1}{8}$ " braided nylon rope
- 40' of  $\frac{3}{16}$ " braided nylon rope
- 1 roll electrical or other tape
- 1 roll flag tape

### Tools and Reusable Supplies

- 1 lb. 8d box nails
- 1 8' step ladder
- 1 caulk gun
- 1 heavy hammer
- 1 tape measure
- 1 nail apron
- 1 pr. scissors
- 1 drill with  $\frac{1}{4}$ " and  $\frac{13}{64}$ " bits

### Procedures

**Prepare EMT, ropes, and stakes.** Cut one of the lengths of  $\frac{3}{4}$ " EMT into four 2.5' pieces. Cut one of the lengths of  $\frac{1}{2}$ " EMT into three 40"

pieces; from the other, cut one 40" piece and two 20" pieces. Cut the  $\frac{1}{8}$ " rope into seven 13.5' pieces and two 12' pieces. Cut the  $\frac{3}{16}$ " rope into two 20' pieces. Use a lighter or blow torch to melt the ends of the  $\frac{1}{8}$ " ropes. Pull each melted end to a point to aid in threading the rope through snug holes. (Warning! Melted nylon is hot and sticky. Protect your fingers by using leather gloves or thick layers of cloth.) Melt the ends of the  $\frac{3}{16}$ " ropes to prevent unraveling. To finish the stakes, drill a  $\frac{1}{4}$ "-dia hole about 1" from one end of each 20" piece of  $\frac{1}{2}$ " EMT. Insert and fasten a 1  $\frac{1}{4}$ " machine bolt in each hole—to prevent the guy ropes from slipping off the tops of the stakes.

**Make support poles.** Make 12.5' support poles by joining 2.5' pieces of  $\frac{3}{4}$ " EMT with 10' pieces. The segments are joined by an internal splint made of a 40" section of  $\frac{1}{2}$ " EMT. To prepare the splints, wrap the four 40" pieces of  $\frac{1}{2}$ " EMT with tape at each end and at 1" on either side of the midpoint (Fig. 1D, splint). At each of the four wrapping places on each piece the tape should increase the diameter of the EMT so that it will slide snugly into both to-be-joined pieces of  $\frac{3}{4}$ " EMT. Join each 2.5' piece of  $\frac{3}{4}$ " EMT to one of the 10' pieces by slipping a wrapped 40" piece of  $\frac{1}{2}$ " EMT 20" into the two pieces to be joined (Fig. 1D, splice). Drill a  $\frac{11}{64}$ " dia hole through the assembly at 1" on each side of the junction of the pieces of  $\frac{3}{4}$ " EMT. Secure with two  $1\frac{1}{4}$ "  $\times$  10–32 machine screws. Designate two of the support poles as eves poles and two as rear poles. Make the 2.5' segment the upper end of each pole.

Measuring from the top of each eves pole, drill a  $\frac{1}{4}$ "-dia hole at 12". In the same plane, drill  $\frac{13}{64}$ "-dia holes at 0.5, 13, 57, and 149.5" (=0.5" from bottom) (these are for the top, slot, eves, and bottom ropes). Drill, at 90° to the other holes, a  $\frac{13}{64}$ "-dia hole  $\frac{1}{4}$ " from the bottom (for the end rope). Drill the rear support poles like the eves poles, but omit the hole for the eves rope (i.e., the hole 57" from the top).

**Assemble and erect the frame.** Insert a 3" eye bolt through the  $\frac{1}{4}$ " holes to join the eves and rear poles of each end of the frame. Place a washer at the eye, between the poles, and next to the nut. The eyes establish the outside of each end, and one end must have the eves pole on the outside and the other must have it on the inside. Lay the ends on the ground several feet apart, one with outside (=eye-side) up and the other with outside down. Slightly spread the poles of each end making the front and rear poles of each end parallel to the corresponding pole of the other. Now thread the seven 13.5' pieces of rope through corresponding holes of the two ends being careful not to cross the ropes and to thread the ropes from the inside of the ends. To secure the ropes to the support poles, tie an overhand knot in each end, leaving a tail of about 1". Thread the two end ropes into the bottommost holes and



secure them in the same way as the cross ropes. Attach a  $\frac{3}{16}$ " guy rope to each eye.

Drive the two stakes into the ground ~40' apart. With one person on each end, erect the support poles with eyebolt eyes outward. Open the end poles into A's, being careful to face the two eves poles in the same direction. Tie the guy ropes to the stakes. Check the cross ropes and end ropes for problems—viz., wrong insertions and crossed ropes. Undo, rethread, and retie as required. Use guy ropes to pull cross ropes taut and move poles to tighten end ropes and to square the frame in all its planes.

**Apply the netting.** Cut the netting into one 19' and two 11.5' lengths. Starting at the bottom rear of the trap, thread the 19' piece up between the slot ropes, outside and over the top ropes, and back down between the slot ropes. Once threaded, spread the netting laterally, and starting at the lower rear corners temporarily attach it around the frame, to itself, using 8d box nails as you would straight pins in cloth. Pull the netting around the bottom cross rope making a 1" hem. At intervals of ca. 6" insert two nails parallel to the rope and  $\frac{1}{8}$ " and  $\frac{3}{4}$ " from it. Pull the netting around each rear pole and insert nails at ca. 6" intervals. Continue to the top of the trap and then down the eves pole. Upon reaching the eves, hem the netting around the eves rope in the manner described for the bottom rope. Now put a bead of silicon caulk between each pair of nails in the two hems, being careful to ensnare both layers of netting.

Wrap the selvage of an 11.5' piece of netting around each end rope and use nails to hem as before. Temporarily attach the middle of the opposite selvage to the eye near the top of the trap. Now work from the bottom and stretch the netting between eves pole and rear pole. Use nails to tack it to the main net and around the lower portion of the eves pole. Make your work easier by cutting off surplus netting (as it becomes apparent what is surplus). Once you have the netting on each end loosely fit and trimmed, remove and reinsert the nails as you pull it tight for the final fit. When you have all the netting in place and stretched except for two small triangles that close the ends of the duct, glue the netting to the support poles with a bead of silicon running the full length of each pole. When the silicon has congealed, remove all nails.

Take two scraps of netting and use nails to sew them to each end of the duct. Loosely trim the netting and stretch the triangles so that they can be glued with silicon to the poles on either side and to the selvage of the main net above. When you apply the silicon be sure to close any holes (=potential butterfly exits) that remain where the main net changes from one support pole to another. When the silicon has congealed,

remove the nails. Then check again for holes larger than the  $\frac{3}{8}$ " mesh of the netting and close them with silicon.

To make the netting visible to persons working around the trap, tie 1' lengths of flag tape to the netting at 2' intervals at 4' above the ground.

**Striking, transporting, erecting, and servicing the trap.** To strike a trap, a person at each stake unties the guy rope and keeps it taut as he/she walks toward the trap. Upon reaching the trap, each grabs a rear pole and tips the top forward causing the rear and eves poles to scissor shut while making sure the end netting tucks inside the closing poles. The support poles are then held horizontally with the main net stretched between and the guy ropes thrown toward the center. The two strikers walk toward each other as each rolls the netting around two folded poles. When the rolls meet near the center, one takes both rolls. The struck trap can now be transported on one person's shoulder. The rolls can be secured with a bungie cord or rope.

To erect a trap, two persons reverse the striking process, being careful not to tear the netting as it unrolls. Unless the end of the eye bolts and the splint-securing machine screws have been cut off and filed, the netting may have to be extricated from them. Drive stakes 45' apart along a line that is perpendicular to the mean direction of migration. If there are not two bowlines in each guy rope, tie them now—first one to make the eye-to-stake length 18.5' and then one to make that length 24'. Now erect the trap making sure that it is square, centered between the stakes, and facing into the migratory stream. With the inner bowline of each guy rope around a stake, the trap's cross ropes should be properly taut. If they are not, adjust one of the bowlines.

To remove butterflies from the trap, partially collapse it by releasing the guy on one end until its outer bowline is holding the trap. Butterflies in the two thirds of the duct closest to that guy should now be easily reached. Restore the trap and collapse it in the other direction to reach butterflies in the rest of the duct.

## GENERAL NOTES

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### STICKY INTEGUMENTAL COATING OF A DALCERID CATERPILLAR: A DETERRENT TO ANTS

**Additional key words:** Chemical defense, *Dalcerides ingenta*, Lepidoptera, larva, *Camponotus floridanus*.

Dalceridae are a small group (85 species) of mostly neotropical moths with sluglike larvae covered with a gelatinous coating (Dyar 1925, Hopp 1928, Stehr & McFarland 1987, Miller 1994). Nothing was known about the chemistry or function of this coating, although it had been proposed to serve for defense (Stehr & McFarland 1987). We here present evidence, based on staged encounters between a dalcerid caterpillar and ants, that the larval coating can indeed serve as an effective deterrent to attack.

The larvae were offspring of gravid females of *Dalcerides ingenta* (Hy. Edwards), the only species of Dalceridae native to the United States, collected at Ash Canyon in the Huachuca Mountains, Cochise County, Arizona. They were raised on mature foliage of one of their host plants, *Arctostaphylos pungens* (H.B.K.) (Ericaceae), as well as on leaves of various oaks [*Quercus emoryi* Torrey (Fagaceae) figures in the moth's natural diet]. Voucher specimens of adults and larvae are deposited in the entomological collection of the National Museum of Natural History, Washington, D.C.

The dorsal investiture of *D. ingenta* has the warty appearance (Fig. 1) characteristic of dalcerid larvae (Dyar 1925, Stehr & McFarland 1987). The investiture is moderately sticky and can be readily pulled from a larva by rolling it onto a glass rod (Fig. 2). Pulling on a single wart with forceps typically results in detachment of a string or cluster of warts (Fig. 2). If a larva is artificially denuded by removal of the entire complement of warts, a coating of semi-liquid material is exposed (Fig. 1).

The ants used in the encounters were from a laboratory colony of *Camponotus floridanus* (Buckley) (Formicidae), originally taken near Lake Placid, Florida. We previously had used this species in predation experiments with other insects (Eisner 1972).

The tests were carried out in 15 × 50 mm glass petri dishes. For each test, a number of ants (5-10) were first added to a dish, following which a piece of *Quercus* leaf was introduced bearing a single *D. ingenta* larva. Events were monitored with a Wild M400 photomicroscope and were consistent for each of the 5 larvae tested. Ants repeatedly came in contact with the larvae and inspected these with antennae and palps, but in most cases they withdrew without attempting to bite. There was no evidence of repellency on near contact. Ants seemed to back away from larvae only after directly palpating them. Actual bites or attempted bites occurred only in a few cases, but the results in these instances were dramatic. Ants either became temporarily stuck to the larval coating and had to struggle briefly to free themselves, or they pulled away quickly, but with their mouthparts encumbered by detached dabs of coating (Fig. 3). Such ants never persisted in their assault, but engaged instead in protracted, eventually successful, cleansing activities.

Two samples of coating, each representing strippings from several larvae, were extracted respectively with methanol and ether, and examined by gas chromatography (using a non-polar liquid phase). No evidence was obtained of presence of volatile or volatilizable components. Given that the coating appeared to effect its deterrence by mechanical action rather than repellency, this finding was perhaps to be expected.

Caterpillars possess a multiplicity of chemical defenses, including eversible (Brower 1989) and dischargeable glands (Attygalle et al. 1993), urticating spines (Kawamoto & Kumada 1984), and glandular hairs (R. Rutowski & T. Eisner personal observation, *Eurema* and *Pieris*). In addition, some derive protection from forcible emission of enteric

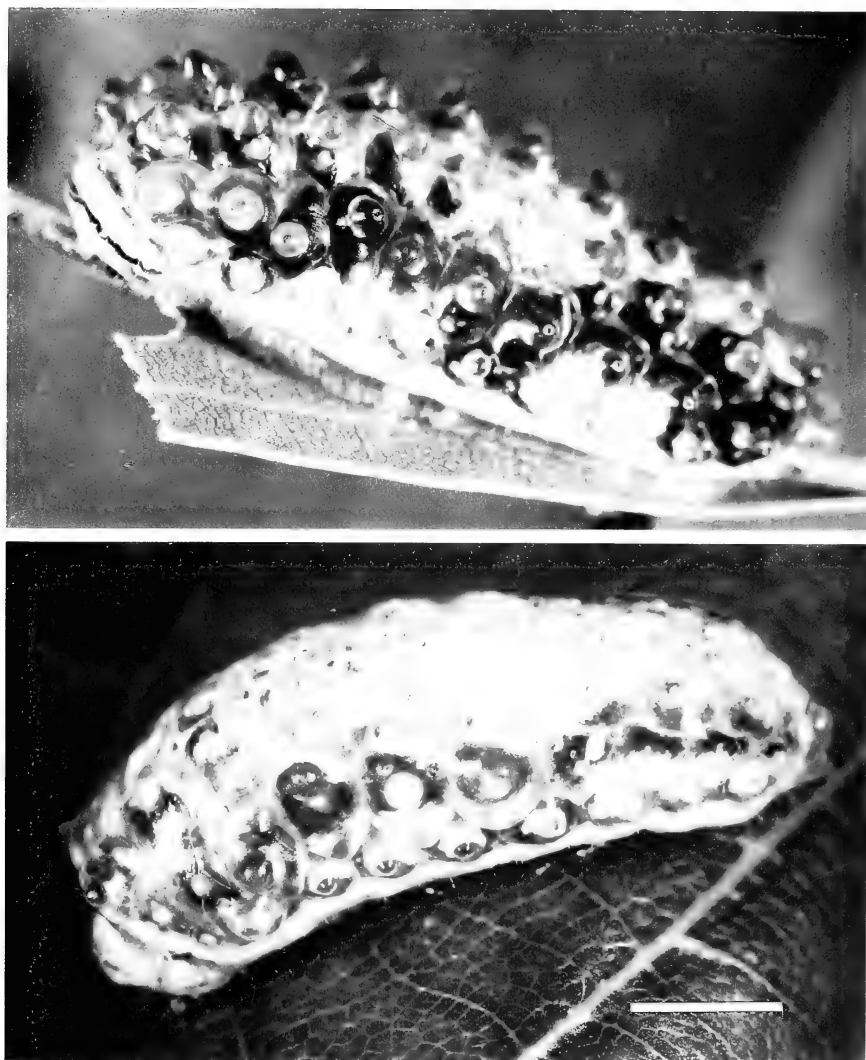


FIG. 1. Typical larva, showing rows of dorsal gelatinous warts (top). Larva from which middorsal warts have been removed, exposing the semi-liquid material beneath (bottom). [Scale bar = 2 mm]

fluid (Smedley et al. 1993) or possession of systemic toxins acquired from the diet (Bowers 1993). To our knowledge, dalcerid larvae are exceptional among caterpillars in possessing a sticky integumental coating, essentially comparable to that of slugs (Mollusca: Gastropoda). *Olona* spp. of the family Limacodidae, a group related to the Dalceridae, also possess a gelatinous coating (Holloway et al. 1987). The integument of molluscan slugs has itself been shown to be deterrent to ants (Eisner 1970). Sticky integumental coatings are generally rare among insects. They occur in certain sawfly larvae (*Caliroa* spp., Tenthredinidae), in which they also may be defensive, although there appears to be no evidence to that effect (Nordin et al. 1972). In some cockroaches, the last abdominal

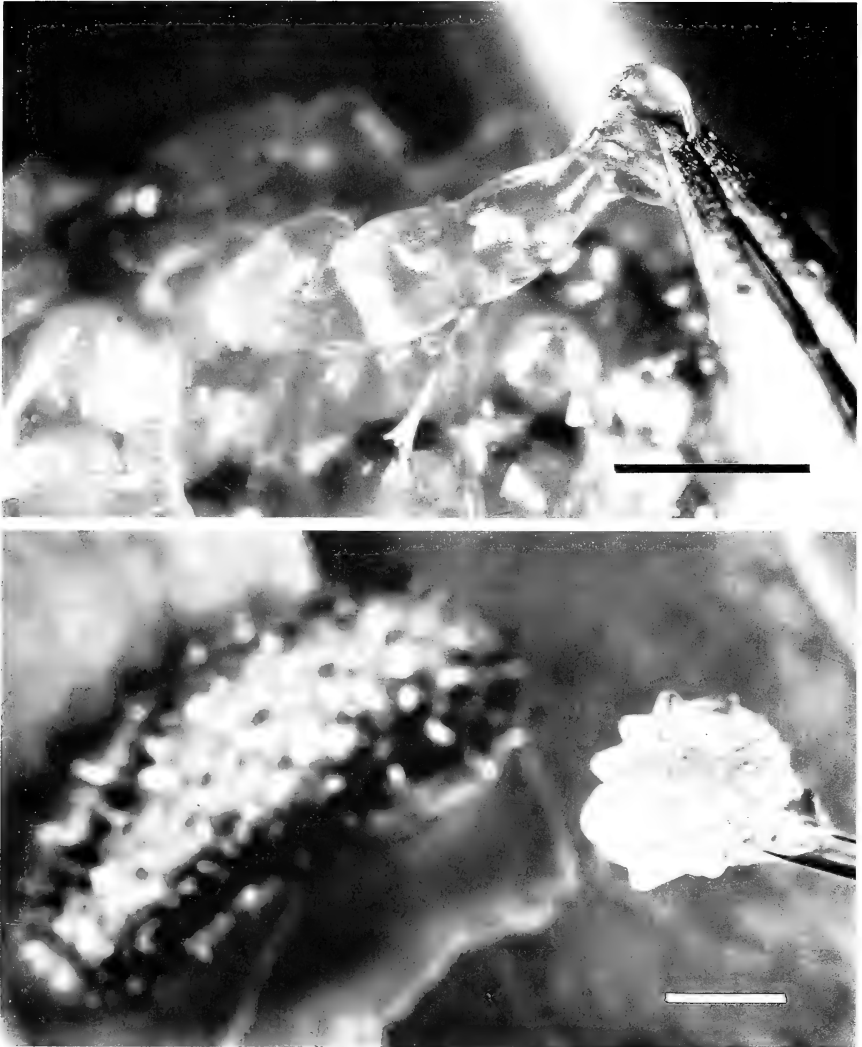


FIG. 2. A "wart" has been grasped with forceps and is being pulled away, causing a strand of warts to be detached from the investiture (top). A cluster of warts has been taken up by a glass rod; to remove the cluster the rod was pushed into the investiture and slowly rolled (bottom). [Scale bars: top = 1 mm; bottom = 2 mm]

tergites are covered with a proteinaceous slime of proven physical deterrence to ants (Plattner et al. 1972). A number of arthropods produce sticky secretions as products of dischargeable glands. Examples include certain syrphid fly larvae, which protect themselves by use of a viscous glue that they discharge from salivary glands (Eisner 1972), and geophilid centipedes, which eject a proteinaceous cyanogenic slime when disturbed (Jones et al. 1976). A classic example is that of onychophorans (*Peripatus* and its relatives),

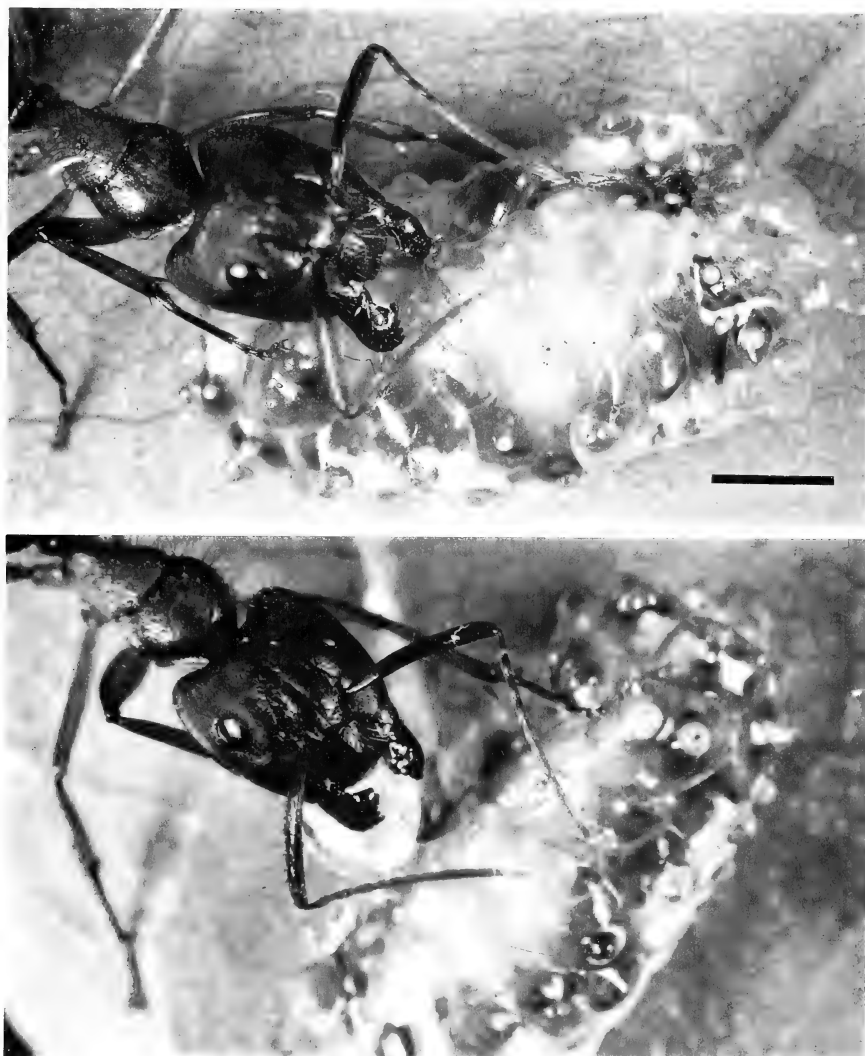


FIG. 3. *Camponotus floridanus* biting a larva; the left mandible has become entangled in the sticky slime (top). *Camponotus floridanus* backing away after having bitten into the larva's investiture; a wad of slime has become stuck to the ant's mouthparts (bottom). [Scale bar = 2 mm]

which eject aimed jets of a rapidly hardening glue from a pair of cephalic glands (Alexander 1957, Eisner 1970). The fluid literally cements attacking ants and spiders to the substrate when these are hit by the spray (Eisner, unpublished laboratory observations with unidentified onychophorans from Panamá).

Insufficient *D. ingenta* were available to determine precisely how the integumental coating is engendered. Evidence presented so far about the presumed underlying secretory

mechanism suggests that the coating may consist in part of sloughed integumental layers (Hopp 1928).

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#### HOST PLANTS OF *POANES MELANE* (HESPERIIDAE)

**Additional key words:** grasses, Poaceae, skipper, biology.

*Poanes melane* (Edwards), the umber skipper [formerly *Paratrytone melane* (Burns 1992)], is found along the Coastal Range of California and in the foothills of the Sierra Nevada. In rural areas adults are found in grassy habitats along streams and in forests (Emmel & Emmel 1973). This species is common in urban and suburban areas, most likely because its host plants (grasses; Poaceae) are abundant and well-maintained in lawns (Heppner 1972, Brown 1984). This source of host plants could become especially important during the summer generation, a dry season in California when many grasses are no longer green. *Poanes melane* larvae are known to feed on several C<sub>3</sub> and C<sub>4</sub> grasses, including *Cynodon dactylon* (L.) Pers. (C<sub>4</sub>), *Deschampsia caespitosa* (L.) Beauv. (C<sub>3</sub>), *Lamarckia aurea* L. (Moench) (C<sub>3</sub>), and *Stenotaphrum secundatum* Kuntze (C<sub>4</sub>), and one sedge (Cyperaceae), *Carex spissa* Bailey (Brown 1984, Scott 1986).

Adult female *P. melane* lay eggs singly on the undersurfaces of grass blades. The mature larva is approximately 30 mm long with a brown head and dusky yellow-green or tan body mottled with black punctations of varying sizes (Comstock & Dammers 1931, Emmel & Emmel 1973). Larvae have a blackish mid-dorsal line, a cream lateral stripe, and three dark lines on each side (Scott 1976). Larvae also construct tubular shelters by tying two or more leaves of their host plants together with silk or by rolling single broad leaves into tubes secured with silk along their edges. Mature larvae feed nocturnally, generally at the distal ends of tied or rolled leaves. This association between shelter formation and feeding activity was used in several cases in this study to determine the use of host plants by *P. melane*. I report here several new host records from Berkeley, California made during a four year study of the relative performance of *P. melane* larvae on C<sub>3</sub> and C<sub>4</sub> grasses. All plants used in feeding experiments were grown from seed available commercially or from the U.S. Department of Agriculture Soil Conservation Service, unless otherwise noted.

*Poanes melane* larvae were observed feeding on a hedge of bamboo, *Phyllostachys bambusoides* Sieb. and Zucc. (Poaceae, C<sub>3</sub>), for three generations in 1985 and 1986. Complete development to adults was inferred from the presence of pupal cases in larval shelters. Oviposition by adults on *P. bambusoides* was observed on several occasions in the field.

*Ehrharta erecta* Lam. (Poaceae, C<sub>3</sub>) is commonly used by larvae in the field (observed from 1985 to 1989). In laboratory experiments, *P. melane* grew well on *E. erecta* grown from seed collected in the field (Barbehenn and Bernays 1992). Oviposition was observed on several occasions on *E. erecta* in the field.

Late-instar larvae were observed feeding on *Lolium multiflorum* Lam. (Poaceae, C<sub>3</sub>) on two occasions in 1985. Adult *P. melane* (one male and one female) were reared from these larvae. *Lolium multiflorum* also supported growth to adulthood in laboratory experiments (Barbehenn and Bernays 1992), and adults in 0.5 m<sup>3</sup> cages readily oviposited on potted plants. However, in two subsequent years larvae fed one-month-old *L. multiflorum* commonly rejected it or were unable to grow.



*Poanes melane* larvae (n=4) were collected on *Paspalum dilatatum* Poir. (Poaceae, C<sub>4</sub>) in March 1985 (Elizabeth Bernays pers. comm.). Larvae were successfully reared on *Paspalum dilatatum* in several laboratory experiments (Barbehenn and Bernays 1992).

*Pennisetum clandestinum* Hochst. ex Chiov. (Poaceae, C<sub>4</sub>) was commonly oviposited on in the field. In the laboratory this coarse grass supported good larval growth (Barbehenn and Bernays 1992). *Pennisetum clandestinum* was grown from plants collected in the field.

*Sorghum sudanense* (Piper) Stapf. (Poaceae, C<sub>4</sub>), planted in a mixed stand with *C. dactylon*, *P. clandestinum*, and *E. erecta*, was commonly oviposited on by adults flying in a 13×7×3 m outdoor screen cage in 1986 and 1987. Larvae grew rapidly on *S. sudanense* in laboratory experiments (Barbehenn and Bernays 1992).

One case was observed in February 1987 of a mature larva feeding on *Hordeum leporinum* (Link) (Poaceae, C<sub>3</sub>). Later efforts to rear *P. melane* on this species were unsuccessful, however. Fourth-instar larvae commonly rejected *H. leporinum* leaves from plants grown from seed collected in the field.

*Digitaria sanguinalis* (L.) Scop. (Poaceae, C<sub>4</sub>) was found to be an acceptable host plant, both for oviposition in the laboratory and for larval growth (Herbert Baker pers. comm.). The source of these plants was not determined.

Scott's (1986) listing of *Bromus carinatus* as a host plant of *P. melane* is based on a field observation by John Lane of oviposition on this species (Langston 1980). Two additional records reported here confirm that *B. carinatus* is used by *P. melane* adults and larvae. Several mature larvae were found on this species in March 1985 (Junji Hamai pers. comm.) and a female was observed ovipositing on *B. carinatus* in the Berkeley Hills in May 1985 (John Brown pers. comm.).

In addition to the above observations of host use by *P. melane*, the ability of larvae to use several novel grass species was tested. Larvae were reared on *C. dactylon* through three instars and then fed the following grasses during the fourth instar: *Dactylis glomerata* L. (potted plants from the field), *Agrostis palustris* Huds., *Festuca myuros* L., *Festuca rubra* L., and *Agropyron cristatum* (L.) (all C<sub>3</sub> Poaceae). Larvae were successfully reared on each of these species (Barbehenn and Bernays 1992). Finally, *Poa pratensis* (L.) (Poaceae, C<sub>3</sub>) was readily accepted by larvae, but it was not determined whether larvae develop successfully on this species.

In addition to certain plantings of *L. multiflorum* and *H. leporinum*, three grasses were found to be unsuitable as hosts for *P. melane*: *Panicum virgatum* (L.), *Panicum amarulum* (Hitch. & Chase), and a native coastal grass *Muhlenbergia rigens* (Benth.) Hitch. (all C<sub>4</sub> Poaceae). Larvae (n = 3 per species) consistently rejected the *Panicum* species. *Muhlenbergia rigens* was readily accepted by larvae (n = 15) but did not support growth. The unusually tough and thick leaves of *M. rigens* is a possible factor limiting its use by *P. melane*.

With the exception of *D. caespitosa* and *B. carinatus*, all of the grasses previously reported as host plants for *P. melane* are introduced species. In addition, all of the new host plants reported here are introduced species. As noted by Brown (1984), few native host plants of *P. melane* are known. Given the acceptability of a wide variety of grasses as host plants, it seems likely that *P. melane* originally fed on a variety of native grasses before the spread of introduced grasses in California. The acceptability of a wide variety of grasses by *P. melane* also suggests that the "indiscriminate" oviposition on grasses by captive females (Comstock & Dammers 1931) and a free-flying female (Brown 1984) may represent a viable egg-laying strategy.

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## COMMENTS ON THE NATURE AND ORIGINS OF MIGRATIONS OF LEPIDOPTERA TO BERMUDA

**Additional key words:** evolution, migratory cues.

"The Lepidoptera of Bermuda" (Ferguson, Hilburn & Wright 1991), which I recently reviewed for this Journal (Gaskin 1993), includes an interesting essay in the Appendix which, for brevity, I refer to below as Ferguson (1991). In this, he discussed a number of problems and paradoxes concerning the nature and origins of the long-distance migrations of Lepidoptera to Bermuda, stimulating the additional thoughts and comments presented in this note.

I will start by summarizing the general findings of Ferguson et al. (1991): Bermuda is an oceanic archipelago, dominated by one large island, that caps a seamount with no earlier geological connections to the North American mainland. This archipelago supports a disparate, super-saturated lepidopterous fauna, assembled by over-water dispersal at various times during the last five hundred thousand years, from southeastern North America and the northeastern Caribbean. A small number of endemic species are recognized, derived from ancestors in these two regions. The remaining members of the Bermudian fauna are morphologically and probably genetically, similar to their source populations.

The biomass, diversity, and composition of the Bermudian fauna must have undergone dramatic increases and reductions during the Quaternary concomitant with several radical fluctuations in the surface area of the archipelago.

It was not the primary purpose of Ferguson and his co-workers to develop hypotheses concerning the role that interactions of environmental stimuli, physiology, and behavior might have played in the evolution of long distance migrations of Lepidoptera to Bermuda. Certainly, the phenomenon appears to pose problems for the evolutionary geneticist. If there is no demonstrable return flight, then there seems to be no way for the trait to be fed back into the source population, and no cumulative selection from one generation to the next (Ehrlich 1984). Some of the Lepidoptera which migrate frequently to Bermuda have near-global ranges, and are found also on other oceanic islands. Others have close relatives in widely distant regions with similar migratory behavior. Ferguson estimates

that the migrants to Bermuda make nonstop flights of more than 1000 km, often using lower altitude elements of the jet stream. A number of species from the southeastern United States found on Bermuda also make well-documented annual migrations into the northern states and Canada. Overwintering is unlikely in such cases because these species do not exhibit diapause. Ferguson speculates that many of these make return southern flights within continental North America that have not yet been detected. Presently the best known two-way migration within North America of course, is that of the monarch butterfly (*Danaus plexippus* L.; Nymphalidae). The movements have been copiously documented and the basic elements of the migration have been known for many years (Urquhart and Urquhart 1978). Northward spring flights in North America by species of *Vanessa* are also well known (Scott 1986). In 1992, for example, I counted about 125 *V. cardui* and *V. virginiensis* moving through one small part of Guelph, Ontario, Canada within about 4–5 hours on 26 April, pausing to nectar at clumps of spring dandelions on small patches of waste ground. Weaker southward return flights by *V. cardui* have been observed during late summer and fall in various parts of the United States (Scott 1986). There are also recent reports of consistent southerly autumn movements of *V. atalanta* in the United Kingdom (Riley & Riley 1992). Naturally, these observations may reflect only the prevailing wind direction at the time. Without resorting to mass alar tagging, it is exceedingly difficult to prove conclusively that observed movements of butterflies are in fact part of a large-scale migration rather than periodic local activity. It is, alas, quite unlikely that the kind of observer effort generated for the monarch butterfly programs could be duplicated for large-scale tagging of cutworm moths.

Recent advances in methods to identify and trace specific combinations of isotopes through food chains may give us an additional indirect way of detecting long-distance migrations. Systematic sampling of mtDNA and nDNA in given species at different localities also may provide insight into population structure and movements. Unfortunately, absolute methods for satisfactorily distinguishing sampled entities at the population level have yet to be perfected for animal species, despite great success in individual DNA “fingerprinting.”

There are other ways of viewing the problems posed by Ferguson, however. It is rarely clear what proportion of any insect population migrates. We probably have more data on the migration of *D. plexippus* than for any other butterfly or moth, but some aspects are still unclear. Although huge numbers of monarch butterflies migrate from the southern wintering grounds into the northern United States and Canada in normal years, some still can be found even in southwestern Texas in the summer months. It seems unlikely that the migratory instinct is based on an “all or nothing” response in an entire population (Ehrlich 1984). Obviously long-distance return migrations, especially when two generations are involved as in the case of the monarch, demand the transfer of quite sophisticated cue recognition and navigational programming (Baker 1984, Douglas 1986). We have no clear idea of the time scale necessary for such developments.

Ferguson's second puzzle is that the monarch butterflies of Bermuda are now residential, and no longer migrate. The migratory impulse presumably can be over-ridden in some way by internal systems that can recognize specific environmental cues or stimuli of immediate importance to the organism, attention to which will benefit the individual in the short-term and increase its chances of passing on its genetic heritage to offspring. Ignoring for a moment the fact that Bermudian monarchs are on an oceanic island, the question can be seen as part of the more general one “why don't colonial butterflies migrate?” Presumably, the majority tends to remain in the area through repeated exposure to local cues, such as the presence of specific microclimatic conditions or food plants that are absent for some distance around the colony. Statistically, relatively weak fliers carrying out short-distance search movements (random walks) will usually end up back in the locality where the cues are strongest or most repetitive. It is quite normal, however, for some individuals to disperse up to tens of kilometers from a colony. This happens in the case of the European large copper, *Lycaena dispar* (f. *batavus*), for example (Pullin et al. 1993). If such wanderers fail to find their way back and the colony is effectively isolated by unfavorable habitat, then this behavior could potentially threaten the viability of the colony. In other seasons the same behavior might enhance its survival by reducing

pressure on limited food resources. Under normal circumstances, however, in the absence of significant vagility (capacity for dispersal at least to the nearest suitable habitat site), local colonies of a few hundred individuals are certain to be extirpated in the long run by environmental events, often simple density-independent occurrences such as flood, drought, or unseasonable hard frost at some critical point in the life cycle. Stochastic events probably play a greater role in colony extinctions than inbreeding. Dempster (1989) argued that vagility, as a basic attribute, is vital for survival even for butterflies well-adapted to highly specific habitats, because unless isolated colonies are "topped up" at intervals by surplus production from adjacent neighboring units experiencing "good years," they ultimately will disappear. Colonial butterflies in many parts of North America and Western and Eastern Europe have undergone dramatic declines in recent decades (Kudrna 1986). The endangered or threatened species are usually those with rather low vagility, often staying close to localized food plants. This was not such a problem before the advent of drastic modifications to northern temperate ecosystems by the activities of humanity, which have greatly reduced and fragmented previously widespread habitats. Of course, there always were extirpations of colonies by natural processes, with eradications of whole systems during the cold Pleistocene stadials, and some recolonizations in the mild interstadials (Dennis 1976). In the case of species with low vagility, recolonizations of areas were simply a function of expansion of a particular habitat or biotope. Nevertheless, the greater the innate vagility of a butterfly species, the greater the chances of recolonizations, recovery in numbers, and increased opportunities for individuals to perpetuate their genes. Dempster (1989) argued that it was no accident that the butterflies which did not seem to be on the decline in the United Kingdom comprised largely species with high vagility, such as the orange tip, *Anthocharis cardamines*.

In somewhat oversimplified terms, vagility is a basic characteristic of all organisms, providing individuals with options as burgeoning numbers at source increase competition for food supplies. It also improves the chances of meeting and mating with an individual from another parent stock and increasing the heterozygosity of the gene base of the offspring. (To take this any further would lead to a discussion of the value of sexual reproduction.) The ability of individuals on the move to respond to certain environmental cues of immediate importance, such as a change in air temperature, "land in sight," "food in sight," "mate in sight," can over-ride the general stimulus to keep moving. The actual mechanisms that both initiate and cease migration are probably hormonal in nature, even if the basis is genetic.

If there is now no return migration to the southeastern United States by resident monarch butterflies in Bermuda, it may be that the local cues, e.g., somewhat less fluctuation in photoperiod than in New England or southern Canada, or the winter being mild enough for adult survival, may serve to suppress the instinct to leave. Perhaps the prevailing seasonal winds around Bermuda may make it a one-way journey for all immigrant Lepidoptera whatever their migratory indications. Has it been established that *all* Bermuda monarchs are now non-migratory, or is this an assumption (reasonable enough on the face of it) based on monarchs or their immature stages being found there year-round? It would be useful to clarify this point. It also would be interesting to release Bermuda monarchs in critical localities in North America and see what they would do, for example, in the face of a much reduced day-length in central Ontario in early autumn. In a few years time, developments in "wildlife technology" will make radio emitters approaching the size of a pinhead commercially available for this kind of study where mass alar tagging is not appropriate. Prototypes already have been tested.

I think it unlikely that long distance return migrations commonly evolve from long distance one-way dispersals, not just in the case of Bermuda but also on any continental mass. It seems to need too many unlikely events to occur in sequence. Initial returns probably would be accidental. Development of migration in this way would require not only that a few founders somehow find their way back carrying the behavioral trait with them, but also that over a number of generations the survival rate of their offspring should exceed that extant in the general population. In the first few generations the statistical chances of their elimination would seem to be high, unless conditions specifically favorable to the migrators developed quite rapidly in the source habitat.

More realistically, migrations can generally be considered as a survival mechanism evolved, probably during periods of climatic and/or ecological change, as a response to gradual increase in segregation or "de-coupling" of optimal zones for feeding and breeding which had been more closely adjacent in the earlier history of the population. No near-miraculous return flights need be postulated, only slowly widening, short-distance seasonal oscillations. Under these circumstances, natural selection for capacities to navigate and recognize cues could occur with plenty of opportunity for the advantageous traits to accumulate in the population. In the case of the monarch and species with a similar pattern of migration, another vital zone presumably became segregated from both optimal feeding and breeding regions, i.e., that in which the species could survive the winter in the adult stage. Perhaps the monarch already was locked into this type of life cycle, because of critical requirements of one or more of the immature stages that could not be easily modified subsequently. The fact that we see this kind of pattern in a number of the large Holarctic nymphalids suggests that there has been insufficient time for natural selection to favor alternatives other than extension of the seasonal movements and adult overwintering. If we look for distinctly warmer regimes, when the monarch might have been able to overwinter easily at significantly higher latitudes than today, there seem to be three main choices, the rather arid, warm Upper Oligocene, part of the Miocene, or the post-glacial "Warm Period" of about 6,000 years ago. In theory, 5-6,000 generations does not seem an unreasonable time for significant changes in population behaviors to occur, although probably far too short a time for significant changes in biologically important physiology or morphology. The exceptions might include wing color patterns, which often play a role in behavioral responses and recognition and could be subject to quite rapid selection.

My conclusion then, is that the probable answers to the important questions posed by Ferguson in his essay in this monograph are as follows: monarchs and many of the other butterflies and moths that reach Bermuda became long distance migrators on the mainland in response to historical changes in their habitats, much like the migratory songbirds. We don't know when this happened, because behavior does not leave a fossil record. Their original ranges may have been much the same as today latitudinally, but with the critical difference that the adults could overwinter through much of the range instead of only at the southern extremity. The overwintering stage of the life cycle may have been the most critical factor in determining which options were open to selection when conditions changed.

It would be interesting to make some experimental comparisons between the critical factors that appear to operate in such migrations in North America with those in wet-dry season and low-high altitude migrations by Lepidoptera, for example in east Africa and India.

In the case of migrations to Bermuda, the driving forces may be quite incidental; there are some species which have relatively great vagility over land. When these are swept offshore into air masses with a lower level jet stream, they can remain aloft for long periods using the same adaptations that serve when they are over the continent. Because the basic dispersal instinct can be over-ridden by immediate stimuli related to basic survival, they will surely attempt to descend to feed and rest if an oceanic island is located. Prevailing seasonal winds perhaps prevent them from ever returning to southeastern regions of the United States, but it would be exceedingly difficult to determine this conclusively. Additionally, because they have arrived somewhere with resources, the migratory instinct may be suppressed by something as simple as the act of feeding or egg-laying. We have only limited information concerning which hormonal or other physiological releasers and suppressors may be involved. It might be instructive to put aerial nets on ships passing east and north of Bermuda to see what proportion of individuals lift off to fly further. Even rather small species of Lepidoptera, such as *Nomophila* spp. have been recorded far out to sea.

Ferguson's suggestion, that the current high population levels of species such as *Spodoptera* spp. and *Pseudaletia unipuncta* probably result from the relatively recent massive vegetation changes in North America, seems very reasonable. Despite pesticide use, our techniques of crop monoculture assist population growth of some of these insects, and

almost guarantee periodic explosive outbreaks. As these huge populations reduce local resources, dispersal is strongly favored. Even in moderately *r*-selected organisms such as cutworm moths (cf. herring, with eggs in the tens of thousands), traits for dispersal are probably so universal that further intensive selection may not be necessary. The long-term survival problem for these moths, however, is not over when they reach new food sources on a small, isolated island group such as Bermuda. The century or so of change in North American vegetation is clearly not enough time for selection to work in favor of significant decrease in individual fecundity, or the kinds of specialized behaviors evolved in *Heliconius* species in resource-limited tropical habitats (Gilbert 1983). The sedentary island populations of recent origin are still going to be prone to periodic, chaotic population outbreaks and subsequent crashes at times when sources of natural mortality diminish, simply because of their potential fecundity.

This does raise interesting possibilities for other types of research using island Lepidoptera, in addition to the kinds of studies made by Ferguson on migration. Someone might like to examine other aspects of the situation. For example, by looking at related species and genera on islands with biotas of different and preferably known ages, could we test the hypothesis that endemic island Lepidoptera may have evolved lower fecundity rates over time than comparable migrant species, becoming more adapted to the limitations of their food plant and nectaring resources? Alternatively, do the island immigrant populations begin to show more diversity in food plant selection than their continental counterparts?

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CORRECTIONS TO "CHECK LIST OF THE OLD WORLD  
EPIPASCHIINAE AND THE RELATED NEW WORLD GENERA  
MACALLA AND EPIPASCHIA (PYRALIDAE)"

**Additional key words:** *Lepidogma latifasciata*, *Locastra*, *Stericta kiensis*, *Teliphasa dibelana*, *Trichotophya*.

The following are corrections to a list of Old World Epipaschiinae (Solis 1992) discovered after publication. The corrections are listed in alphabetical order as in the original work. Included are several corrections pertaining to the Japanese fauna identified by Inoue (1993). In addition to the corrections listed below, the valid name for the host plant *Eugenia jambolana* Lamarck (Solis 1992:281) should be *Syzygium cumini* (Linn.) (G. Robinson pers. comm.).

*Coenodomus hamptoni* West, 1931: misspelled locality name, should be Palali, not Palili.  
*Epilepia dentatum* (Matsumura and Shibuya, 1927): country should be Japan, not Formosa.

*Lepidogma latifasciata* (Wileman, 1911): it is a **new combination**.

*Lista plinthochroa* West, 1931: misspelled locality name, should be Palali, not Palili.

*Locastra maimonalis* (Walker, [1859] 1859): years are [1859] 1858, and it is a junior synonym of *L. crassipennis* (Walker).

*Locastra crassipennis* (Walker, 1857): senior synonym of *L. maimonalis*.

*Neopaschia nigromarginata* Viette, 1953: locality should be Madagascar Est: Fianarantsoa, not Madagascar, Saigon.

*Odontopaschia economia* Turner, 1913: misspelled species name, should be *ecnomia*.

*Orthaga durranti* West, 1931: misspelled locality, should be Philippine Islands, not Philippines Islands.

*Salma nyctizonalis* (Hampson, 1916a): misspelled locality, should be Philippine Islands, not Philippines.

*Shoutedenidea* Ghesquière, 1942: misspelled genus name, should be *Schoutendenidea*.

*Stericta angulosa* de Joannis, 1929: misspelled locality, should be Vietnam, not Vitenam.

*Stericta angulosa* de Joannis, 1929: misspelled locality, should be Vietnam, not Vitenam.

*Stericta kiensis* (Marumo, 1920): valid species; is not a junior synonym of *Stericta rufescens* (Marumo, 1920), should be placed after *Stericta indistincta*.

*Termioptycha elegans* (Butler, 1881): species belongs in *Teliphasa*, should be placed after *Teliphasa dibelana*.

- Trichotophysa juncundalis* (Walker, 1865): misspelled species name, should be *juncundalis*, and correct year should be 1866.
- Trichotophysa yamatomis* (Strand, 1919): country is Japan, not Taiwan.
- Incertae sedis zophoptera* (Ghesquierer, 1942): misspelled author name, should be Ghesquière.

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- SOLIS, M. A. 1992. Check list of the Old World Epipaschiinae and the related New World genera *Macalla* and *Epipaschia* (Pyalidae). J. Lepid. Soc. 46:280-297.

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## CORRECTIONS TO VOLUMES 47 AND 48

The caption for the cover illustration of 47(2) should have read: "A silverspot butterfly (*Speyeria* sp.) resting beneath the leaf of a fern. Original drawing by Martie Clemons from a photograph by David Liebman."

The correct order of authorship for the article "Clinal variation in *Hesperia leonardus* (Hesperiidae) in the Loess Hills of the Missouri River Valley," which appeared in 47(4):291-302, should be Stephen M. Spomer, Timothy T. Orwig, Leon G. Higley, Gerald L. Selby, and Linda J. Young.

In the article by Astrid Caldas, "Biology of *Anaea ryphea* (Nymphalidae) in Campinas, Brazil," which appeared in 48(3):248-257, the sub-specific name of *Anaea troglodyta borinquenalis* was misspelled as "*borquenalis*" on page 255.

The Editor apologizes for these mistakes and any others that have not been brought to my attention.



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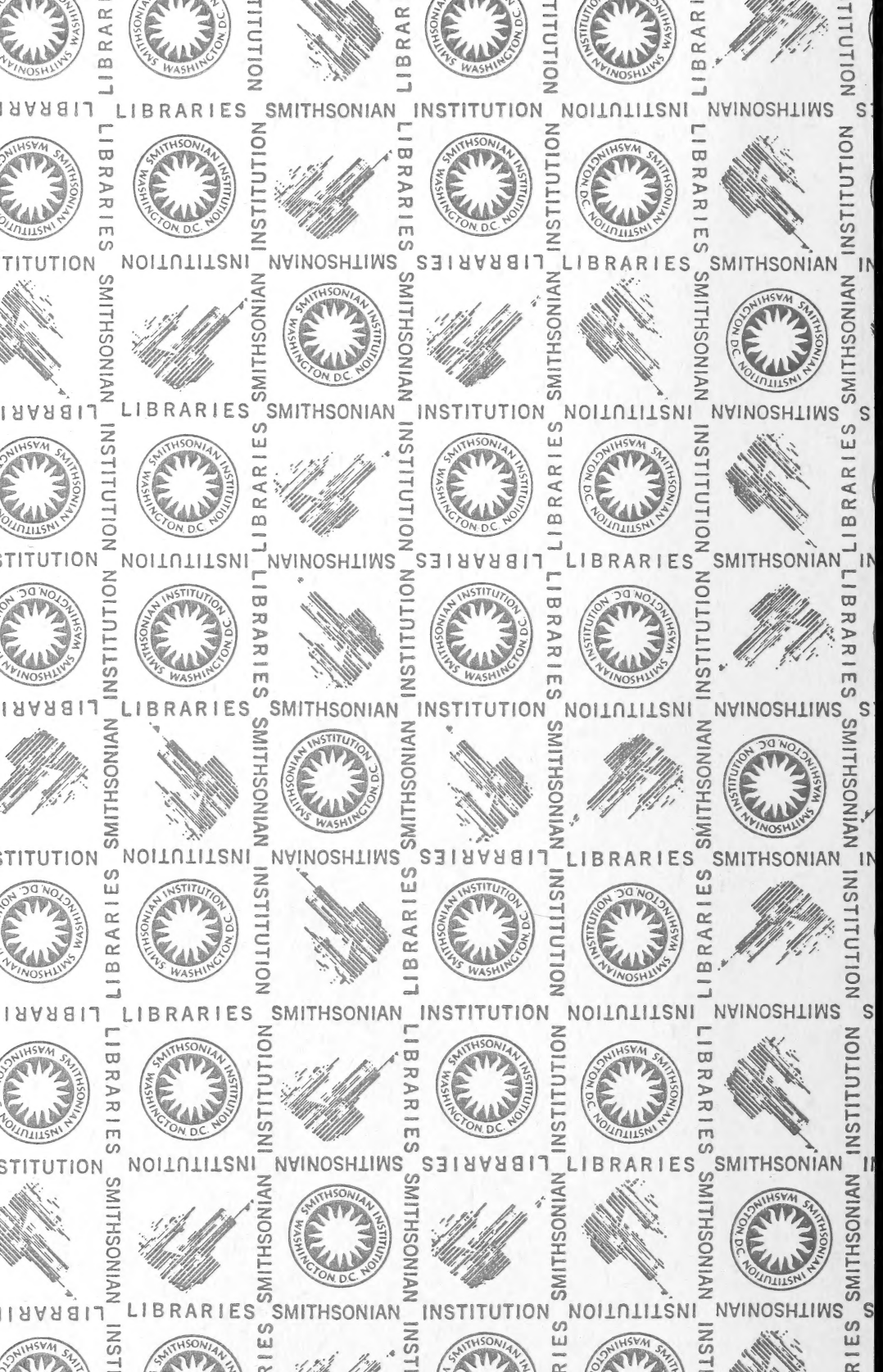
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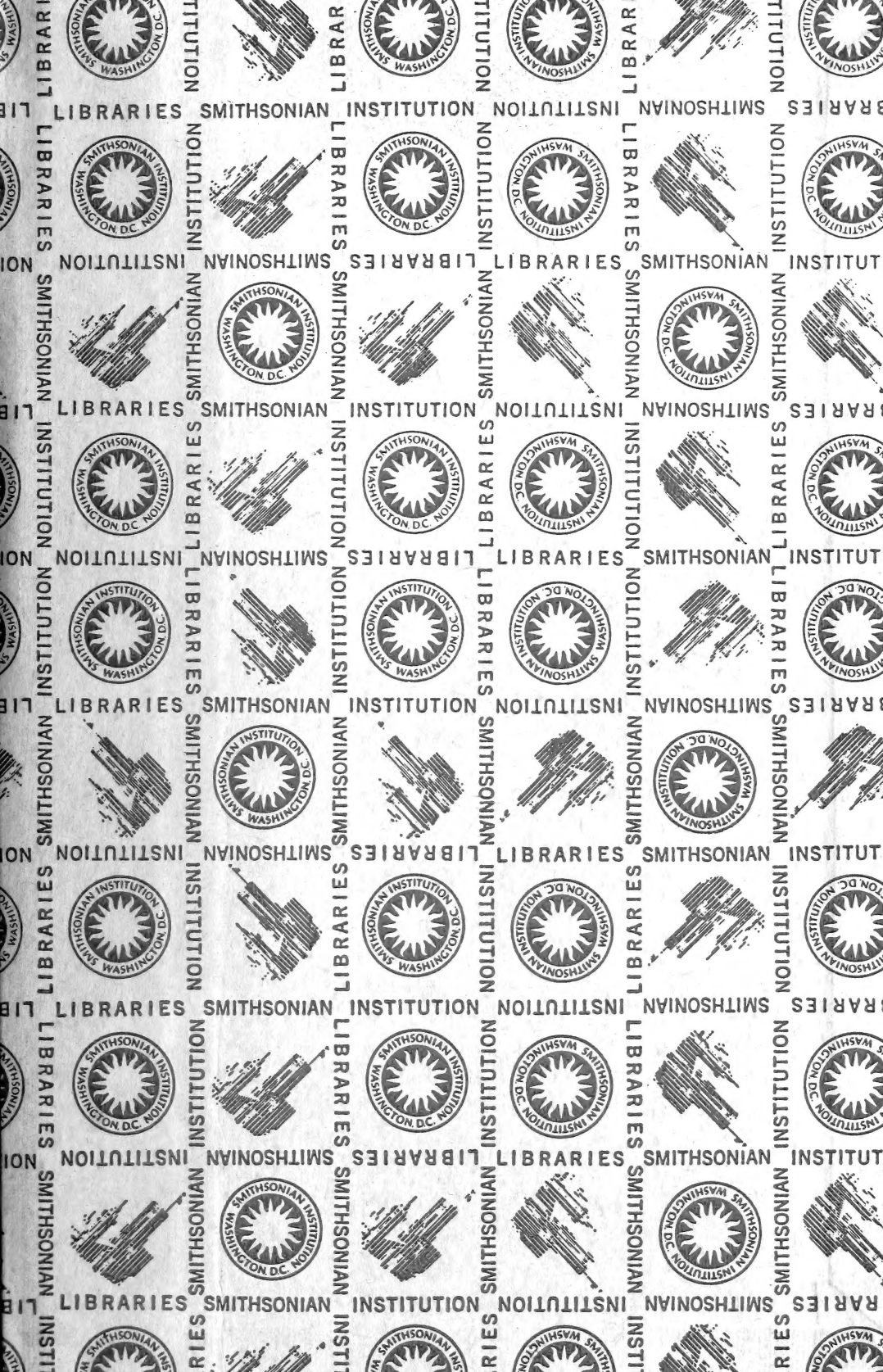
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